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# STUDY ON MODELS OF SINGLE POPULATIONS

by

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C O N T E N T S

# PREFACE

At the Chang Bai Mountain Research Station in Jilin Province in north-east China there is a major research programme on the ecology and management of native forests under the auspices of the Academia Sinica. Prof. Cui Qi-wu has special responsibility for systems analysis in this programme and has spent two years with ITE, at Merlewood and Bangor, developing various aspects of forest ecosystem and management models.

Following an earlier forest management model, Prof. Cui has developed a population model which extends the logistic and exponential equations. The model has general application but has been examined in the context of forest management. The present Research and Development paper is a composite of three papers to provide a full description of the model. The first paper is due to be published in the Journal of Theoretical Biology and describes the basic model, the second describes possible extensions and the third, developed while Prof. Cui was at Bangor, discussed the model as an aid to forest management.

1. An expansion of the logistic and exponential equations by Cui Qiwu and G. Lawson.

2. A new model of population increment with several limiting conditions by Cui Qiwu and G. Lawson.

3. Application: calculation of the control indices used in forest management by Cui Qiwu.

O.W. Heal

# AN EXPANSION OF THE LOGISTIC AND EXPONENTIAL EQUATIONS

Cui Qiwu and G. Lawson

## SUMMARY

Starting with the adsorption theory of chemical kinetics and passing through a number of mathematical transformations, we have introduced a new equation concerning single population increment as follows:

$$\frac{dX}{dt} = U_c X \frac{1 - X/X_m}{1 - X/X'_m}$$

or in its integral form:

$$\ln \frac{X}{X_o} - \ln \frac{X_m - X}{X_m - X_o} + \frac{X_m}{X'_m} \ln \frac{X_m - X}{X_m - X_o} = U_c (t - t_o)$$

This formula connects together the famous logistic equation (often used in ecology) and the equally famous exponential equation (often used in microorganism growth), and is a reasonable model to explain the relationship between population increment and limiting resources. It can be reduced to the logistic equation when the value of $X_m'/X_m$ is very large, and to the exponential equation when the value of $X_m'/X_m$ nears 1. This new equation has three parameters, ie $X_m$, $X_m'$ and $U_c$, and a starting point $(X_o, t_o)$ on the fitting curve. Each parameter has ecological significance.

$X_m'/X_m$ concerns the efficiency of nutrient utilization by an organism. When the value of $X_m'/X_m$ nears 1, the efficiency is high; if the value of $X_m'/X_m$ is large, the efficiency is low and population increment is restricted early by limiting resources.

$U_c$ is a velocity parameter concerning population increment. Its value lies between the value $U_e$ (for exponential growth) and the value $U_L$ (for logistic growth), and is dependent on the value of $X_m'/X_m$. From the velocity parameter $U_c$, we can predict the time course of population incremental velocity (dX/dt), and can observe that it is not symmetrical, unlike that derived from the logistic equation. The maximum difference of maximum velocity between these two equations is 2 times at $X_m'/X_m=1$.

Population growth occurring in nature seems to support the new equation rather than the logistic one, and it has been successfully fitted to various population by means of a least square method.

Key words: Population biology, Ecological model, Limiting resource, Biological kinetics

# 1. INTRODUCTION

The simplest model of single population increment is the well know exponential equation:

$$\frac{dX}{dt} = U_e X \tag{1a}$$

For convenience in the future discussion, it is better written in the integral form:

$$\ln \frac{X}{X_o} = U_e (t - t_o) \tag{1b}$$

where, X and Xo are population densities at t and to respectively; Ue is a velocity parameter in time$^{-1}$.

However, exponential growth can hold true only for a limited period of time, and ultimately an increasing population will exhaust its resources and the life of component individuals. Therefore, to account for the limited supply of resources, another equation is often used to describe the population increment, ie

$$\frac{dX}{dt} = U_L (1 - X/X_m) X \tag{2a}$$

or in its convenient integral form:

$$\ln \frac{X}{X_o} - \ln \frac{X_m - X}{X_m - X_o} = U_L (t - t_o) \tag{2b}$$

where, Xm is the maximum population density allowed by the limiting resource, and can be called the carrying capacity; $U_L$ is the velocity parameter in time$^{-1}$. This is the famous logistic equation which is often used to describe the growth of single populations.

Although the logistic equation has been applied in a wide range of ecological situations, its theoretical hypothesis is too simple and is open to criticism on several grounds:

(A) Equation (2a) is merely the simplest mathematical expression which permits population growth to be halted by a resource becoming limited. It is not derived from a knowledge of an organism's reproduction or nutrient requirements, and has therefore little value in explaining the mechanisms of growth (Smith, 1974; Pielou, 1969).

(B) The relationship between specific velocity (ie dX/Xdt) of population increment and resource availability (expressed as 1-X/Xm) is not necessarily linear. The logistic equation assumes that population growth begins to slow down at half maximum carrying capacity; In reality resource limitation is likely to be proportionately more important in the later stages of population growth and the proposed linear decline is unrealistic.

(C) As t increases, some populations (eg forest plantations with homogeneous age) will grow old, and their incremental velocity will decrease for physiological reasons, even though the resource supply may not be limiting. In other words, $U_L$ should not be a constant, but a function of the population age.

(D) Climatic conditions (water, heat and so on) are limiting factors which are as important as nutrient supply, and the seasonal variation of population increment is especially dependent on the seasonal variation of climate. These two kinds of limiting conditions (ie nutrient and climate) are better discussed separately.

We wish to introduce a new model which includes some ideas on the above points. In special cases, we can reduce the new model to obtain the logistic equation (2a) or (2b) and the exponential equation (1a) or (1b). Therefore, this new model can be considered as an expansion of these two equations. In this paper the model caters for only points A and B, but in paper 2 modifications are introduced to account for senescence and seasonality.

What follows is largely directed towards populations of annual or perennial plants as well as microorganisms, and terms such as 'biomass' and 'nutrient' will often replace 'population density' and 'resource'.

## 2. DEPENDENCE OF THE SPECIFIC VELOCITY OF POPULATION INCREMENT ON RESOURCE AVAILABILITY

In the first instance it is useful to discuss the simplest of all populations: microorganism growth in a tank. Population increment in this case is dependent only on nutrient concentration, and on the ability of the microorganism to absorb nutrients. We can begin from those aspects of chemical kinetics dealing with the adsorbtion of substance onto a surface.

### 2.1 The Adsorption theory in chemical kinetics: The Langmuir isotherm.

Let a substance, at concentration C in gas or solution, be adsorbed at the surface of another phase. Consider unit area of the surface and suppose that a fraction, $\sigma$, is occupied by adsorbed molecules, $(1-\sigma)$ being left free. There is a dynamic equilibrium between free and adsorbed molecules, and this is expressed by the equation:

$$K'C(1-\sigma) = K''\sigma \qquad (3a)$$

where, K' and K" are constants. The left hand side expresses the fact that the rate of deposition of molecules on to the surface is proportional to the amount of free surface and to the concentration of the molecules in the gas or solution; the right hand side shows that the inverse process is proportional to the density of molecules on the surface. Rearrangement of (3a) gives:

$$\sigma = \frac{bC}{1+bC} = \frac{C}{K+C} \qquad (3b)$$

Equation (3b) is know as the Langmuir isotherm (Hinshelwood, 1947), where b=K'/K"; K=1/b=K"/K', in units of concentration. If the adsorbed molecules undergo a chemical transformation at a rate proportional to their density on the surface, then we have:

$$\text{"rate"} = \frac{K_1 C}{K + C} \tag{3c}$$

where $K_1$ is also a constant.

## 2.2 Specific velocity and limiting resources in culture of microorganisms

Equations (3b) and (3c) are forms of Michaelis-Menten equation and have been used successfully in enzymatic kinetics and the culture of microorganisms. Let us take a population of microorganisms as an example. We have the following equation (Mitchell, 1974):

$$U = \frac{U_m C}{K + C} \tag{4a}$$

which is like the above equation (3c), but here describes a process of absorbing nutrients into the microorganism instead of the above adsorption process on the cell surface. Where U is the specific velocity of population increment, ie dX/Xdt, and equivalent to the "rate" in equation (3c); Um is the maximum value of U allowed by the nutrient in the tank, and is equivalent to $K_1$ in equation (3c); C is the concentration of nutrient in the culture medium; K is the value of C needed for U=0.5Um, called the Michaelis-Menten constant.

In this case, the nutrient transfer is from the culture medium to the population. We can use S to express the nutrient per volume which has been absorbed by microorganisms and S' to express the nutrient per volume which remains in the medium and has yet to be utilized by the microorganisms. S' in this case equals C in equation (4a). The total amount of nutrient per volume which can be utilized by microorganisms in the tank, Sm, including that contained in the microorganisms, is a constant, ie

$$S' + S = S_m \tag{4b}$$

Using a dimensionless coefficient, $a$, to translate the nutrient term to population density, we have:

$$S = aX$$

and

$$S_m = aX_m \tag{4c}$$

In other words, S grams of nutrient has been become X grams of population, and Sm grams of nutrient can be become Xm grams of population. Xm is the maximum population density allowed by the nutrient in the tank. Thus from equation (4a), we have:

$$\frac{dX}{Xdt} = \frac{U_m C}{K + C} = \frac{U_m (S_m - S)}{K + S_m - S} = \frac{U_m (X_m - X)}{X_m' - X} = \frac{U_t (1 - X/X_m)}{1 - X/X_m'} \tag{5a}$$

Where: $X_m=S_m/a$; $X_m'=(K+S_m)/a$, and is a parameter related to the efficiency of resource utilization whose significance is discussed later; and $U_c=U_mX_m/X_m'$.

Note two special cases for this new equation:

(A) When the value of $K/a$ is small, then $X_m'=X_m$, and equation (5a) will reduce to become:

$$\frac{dx}{x\,dt} = U_c$$

This is the exponential equation taking $U_c$ (in this equation) as $U_e$ (in equation 1a).

(B) When the value of $K/a$ is large, then $X_m'>>X_m$, and equation (5a) will reduce to become:

$$\frac{dx}{x\,dt} = U_c(1-x/x_m)$$

This is the logistic equation taking $U_c$ (in this equation) as $U_L$ (in equation 2a).

Thus equation (5a) is an expansion of previous two simple equations. When the value of $K/a$ is large or small, it can reduce to original simple equations. However, in general, it is different from those two equations, and it has a reasonable theoretical basis. Thus we can consider equation (5a) as a fundamental model to explain the relationship between population increment and limiting resources.

By integration, we can obtain:

$$\ln\frac{x}{x_0} - \ln\frac{x_m-x}{x_m-x_0} + \frac{x}{x_m'}\ln\frac{x_m-x}{x_m-x_0} = U_c(t-t_0) \qquad (5b)$$

In this form it is easy to see the relationship between the combined model and the previous ones. The first term in the left hand side of equation (5b) is equivalent to exponential hypothesis, and the first two terms together can express the logistic hypothesis. Equation (5b) is unique because of its third term in the left hand side.

The three equations possess different values for their velocity parameters $U_e$, $U_L$, $U_c$. Their relationship will be discussed in section 3. For the moment we can compare the equations by assuming $U_e=U_L=U_c=1$ and plotting the relationship between the specific velocity ($dX/Xdt$) of population increment and resource availability (expressed in $1-X/X_m$). In the combined equation this relationship is non-linear and is dependent on $X_m'/X_m$. (Fig. 1 and Table 1)

TABLE 1. DEPENDENCE OF SPECIFIC VELOCITY (dX/Xdt) OF POPULATION INCREMENT ON RESOURCE AVAILABILITY (1-X/Xm)
(taking Ue = $U_L$ = Uc = 1)

| 1-X/Xm | dX/Xdt from exponential equation | dX/Xdt from equation (5a) | | | | | | | | | dX/Xdt from logistic equation |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Xm'/Xm=1 | 1.2 | 1.4 | 1.6 | 1.8 | 2 | 3 | 4 | 5 | |
| 1.0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| 0.9 | 1 | 1 | .98 | .97 | .96 | .95 | .95 | .93 | .92 | .91 | .9 |
| 0.8 | 1 | 1 | .96 | .93 | .91 | .90 | .89 | .86 | .84 | .83 | .8 |
| 0.7 | 1 | 1 | .93 | .89 | .86 | .84 | .82 | .78 | .76 | .74 | .7 |
| 0.6 | 1 | 1 | .90 | .84 | .80 | .77 | .75 | .69 | .67 | .65 | .6 |
| 0.5 | 1 | 1 | .86 | .78 | .73 | .69 | .67 | .60 | .57 | .56 | .5 |
| 0.4 | 1 | 1 | .80 | .70 | .64 | .60 | .57 | .50 | .47 | .45 | .4 |
| 0.3 | 1 | 1 | .72 | .60 | .53 | .49 | .46 | .39 | .36 | .35 | .3 |
| 0.2 | 1 | 1 | .60 | .47 | .40 | .36 | .33 | .27 | .25 | .24 | .2 |
| 0.1 | 1 | 1 | .40 | .28 | .23 | .20 | .18 | .14 | .13 | .12 | .1 |
| 0.0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

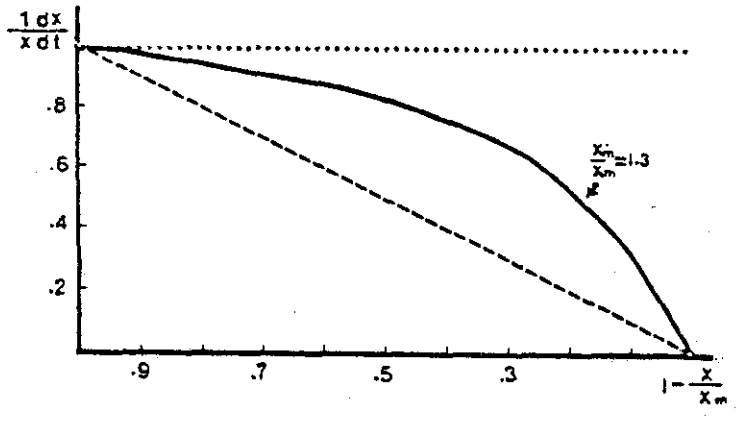


Fig.1. Dependence of specific velocity (dX/Xdt) of population increment on resource availability (1-X/Xm)

.....exponential eq. ------logistic eq. _____ new eq.

## 2.3 Specific velocity and limiting resources in other populations

Under natural conditions, the growth of most populations is not similar to microorganism growth in a tank. However, the process of nutrient absorbtion by plants in the soil may be similar to the uptake of nutrient by microorganisms in a tank. If we use 'biomass' instead of population density and 'soil depth' instead of the depth of the tank (see Fig. 2), then equations (5a) and (5b) will still be true. But in this case, X is the biomass in g/cm²; $X_m$ is the maximum value of X allowed by nutrients in a soil column of depth L(cm), and $X_m' = LK/a + X_m$.

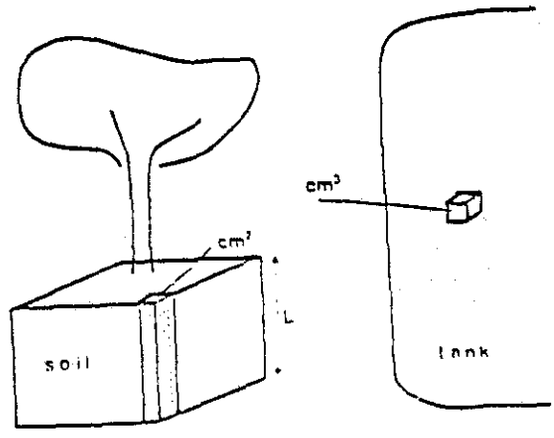


Fig. 2

In nature, plant growth is not only dependent on the nutrient conditions, but also depends on factors such as water, heat and the age or visour of the population. The velocity parameter Uc in equations (5a) and (5b) will be considered, in a subsequent paper, as a function of these other limiting factors.

## 3. BEHAVIOUR OF THE COMBINATION MODEL AND THE BIOLOGICAL SIGNIFICANCE OF ITS PARAMETERS

To illustrate the similarities and differences between the new equation and the exponential and logistic curves it is convenient to assume that each requires the same period of time, $\Delta t_q$, to increment the population from 0.1 to 0.9 of maximum density ($X_m$). In the case of the exponential equation (since $X_m = \infty$) a nine-fold increase is assumed. Thus from equations (1b), (2b) and (5b), we have:

$$\ln 9 = U_e \Delta t_q$$

$$\ln 9 - \ln(1/9) = U_L \Delta t_q$$

$$\ln 9 - \ln(1/9) + (X_m/X_m') \ln(1/9) = U_c \Delta t_q$$

or:

$$U_e = 2.2/\Delta t_q \qquad (6a)$$

$$U_L = 4.4/\Delta t_q \qquad (6b)$$

$$U_c = 2.2(2 - X_m/X_m')/\Delta t_q \qquad (6c)$$

Each equation has a different value of velocity parameter, but Uc (for the combined equation) can vary between Ue (for the exponential equation) and $U_L$ (for the logistic equation), and depends on the quotient $X_m'/X_m$. (Table 2)

TABLE 2. THE VELOCITY PARAMETERS OF THREE EQUATIONS NEEDED FOR POPULATION INCREMENT FROM 0.1$X_m$ TO 0.9$X_m$ DURING THE SAME PERIOD OF TIME (taking $\Delta t_q$ = 2.2)

| Ue(for eq.6a) | Uc (for eq.6c) | | | | | | | | | $U_L$ (for eq.6b) |
|---|---|---|---|---|---|---|---|---|---|---|
| | $X_m'/X_m$=1 | 1.2 | 1.4 | 1.6 | 1.8 | 2 | 3 | 4 | 5 | |
| 1 | Uc= 1 | 1.2 | 1.3 | 1.4 | 1.4 | 1.5 | 1.7 | 1.8 | 1.8 | 2 |

Inserting the above values of Ue, $U_L$, Uc in equations (1a), (2a) and (5a) respectively gives:

$$\frac{dX}{dt} = 2.2\,X/\Delta t_q \qquad (7a)$$

$$\frac{dX}{dt} = 4.4\,X(1-X/X_m)/\Delta t_q \qquad (7b)$$

$$\frac{dX}{dt} = 2.2\,X(2-X_m/X_m')(1-X/X_m)/((1-X/X_m')\Delta t_q) \qquad (7c)$$

Plots of the rate of population increase against population density (Fig. 3) illustrate the relationship between the three equations, and examine the effect of the quotient $X_m'/X_m$.

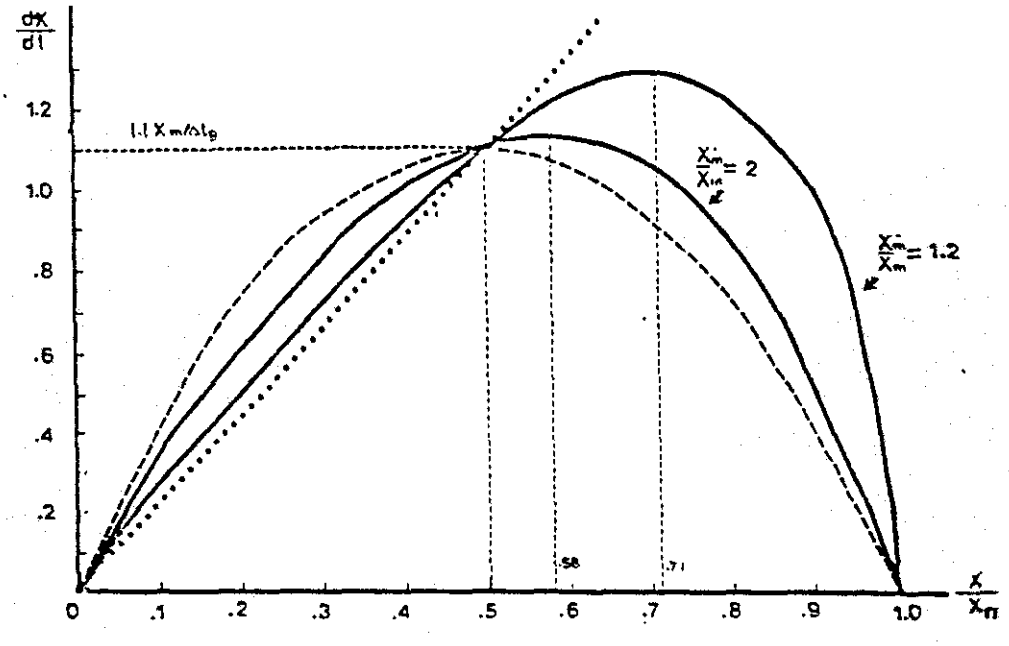


Fig. 3. Velocity distribution of three equations (taking $X_m/\Delta t_q$ =1)

.....exponential eq. ------logistic eq. ——— new eq.

Note, as mentioned before, that in the logistic curve the rate of population increase has a maximum at half carrying capacity (0.5Xm), and declines symmetrically about this point. In the combined equation the rise and fall of dX/dt is not symmetrical and its maximum is not at 0.5Xm, but can instead be obtained by differentiating equation (5a) again:

$$\frac{d(dX/dt)}{dX} = \frac{U_c X_m'[(X_m - 2X)(X_m' - X) + X X_m - X^2]}{X_m (X_m' - X)^2} \qquad (8a)$$

Let equation (8a) equal zero to find the top point Xn of the curve (at this point, dX/dt has a maximum), ie

$$(X_m - 2X_n)(X_m' - X_n) + X_m X_n - X_n^2 = 0$$

or

$$X_m'(2X_n - X_m) = X_n^2 \qquad (8b)$$

The value of term (2Xn-Xm) in the left hand side has to be greater than zero to keep agreement of sign between the two sides of equation (8b). In other words, Xn has to be greater than 0.5Xm, and this was shown in Fig. 3. From equation (8b), we can obtain the values of Xn for different values of the quotient Xm'/Xm, ie

$$X_n = X_m' - \sqrt{X_m'^2 - X_m X_m'} \qquad \text{or} \qquad \frac{X_n}{X_m} = \frac{X_m'}{X_m} - \sqrt{\left(\frac{X_m'}{X_m}\right)^2 - \frac{X_m'}{X_m}}$$

We can substitute these values of Xn into (7b) and (7c) to find the relative values of maximum growth rate at these points. Table 3, for different values of Xm'/Xm (line 2), portrays the maximum velocity (line 4) and the relative population density (line 3) at which this maximum velocity occurs.

TABLE 3. THE RELATIVE VALUES AND PLACES OF MAXIMUM VELOCITY
(taking $X_m/\Delta t_q = 1$)

| | COMBINED EQUATION | | | | | | | | | LOGISTIC EQUATION |
|---|---|---|---|---|---|---|---|---|---|---|
| Xm'/Xm | 1+ | 1.2 | 1.4 | 1.6 | 1.8 | 2 | 3 | 4 | 5 | |
| Xn/Xm | 1 | .71 | .65 | .62 | .60 | .58 | .55 | .53 | .52 | .50 |
| (dX/dt)m | 2.2 | 1.29 | 1.20 | 1.16 | 1.14 | 1.13 | 1.11 | 1.11 | 1.11 | 1.1 |

Most growth observed in nature seems to support the new equation rather than the logistic hypothesis. Microorganisms, plants (Section 5) and animals (D'Arcy, 1952) all evidence a maximum growth velocity when population density is greater than half maximum. Perhaps an extreme case is the Korean-Pine forest (Wang Zhan et al., 1980) where maximum velocity always occurs after one or two hundred years, and Xn is greater than 0.7Xm.

The maximum relative velocity of the combined equation nears that of the logistic one when the parameter Xm'/Xm is greater than 3 (table 3). However, if the parameter

$X_m'/X_m$ nears 1, then the maximum relative velocity of the combined equation is very different to that of the logistic equation. Their maximum difference is 2 times.

From formula (7c), we know that the value of velocity (dX/dt) at the point where X equals $0.5X_m$ is always equal to $1.1X_m/\Delta t_q$ irrespective of the value of $X_m'$. Therefore, it seems that the velocity of population increment at the point of half life, where the population density is $0.5X_m$, is a good parameter for expressing the pattern of population increase. If we derive this value exactly, we can estimate the parameter $\Delta t_q$ which is the time between population density $0.1X_m$ and $0.9X_m$. At $0.5X_m$ we can see that the velocity values for the logistic and exponential formulae (7b) and (7a) are also equal to $1.1X_m/\Delta t_q$ (Fig. 3). Thus, although the distribution of velocity values (dX/dt) is different in the three equations they still have a common value when population density is half of maximum, ie at $0.5X_m$.

Fig. 4 and Fig. 5 express the variation of population density with time using three equations in two different situations: in Fig. 4, velocity parameters ($U_e$, $U_L$, $U_c$) are assumed equal whilst the time ($\Delta t_q$) required for 90% of maximum growth is varied; in Fig.5 $\Delta t_q$ values are assumed equal whilst velocity parameters are varied.

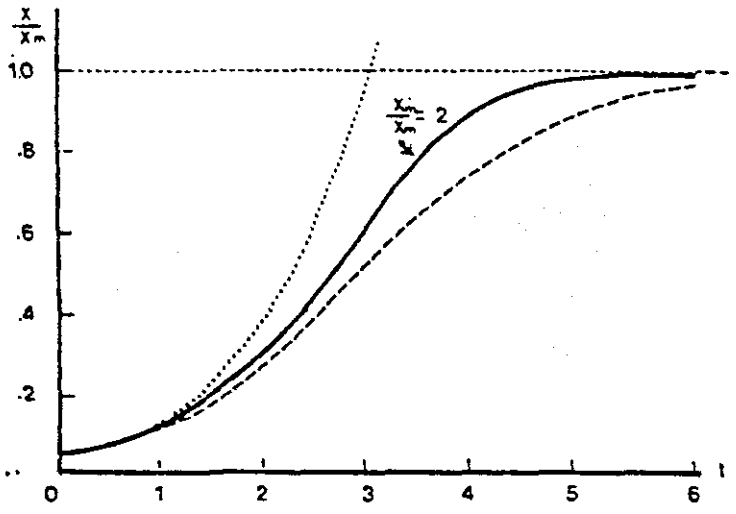


Fig. 4. Variation of population density with the time (taking $U_e=U_L=U_c=1$)

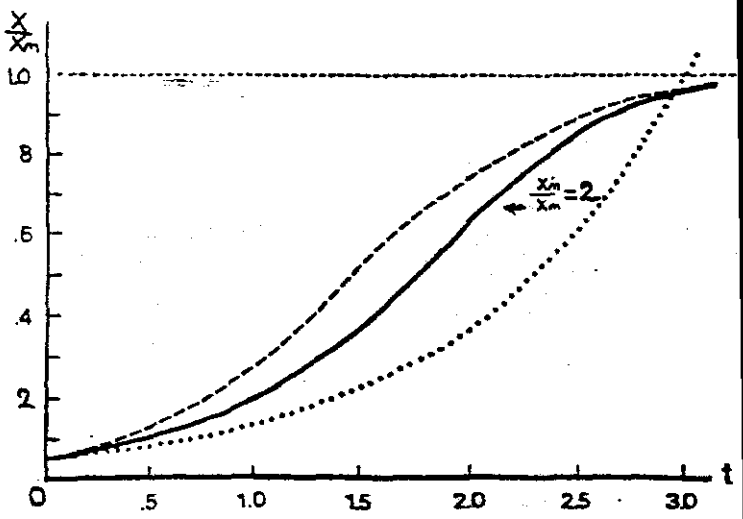


Fig. 5. Variation of population density with the time (taking $\Delta t_q = 2.2$)

.....exponential eq. ------logistic eq. ——— new eq.

It is very interesting to find $X_m'/X_m$ being an important parameter. As the value of $X_m'/X_m$ nears 1, so the curve drawn from the combined equation nears the exponential one. As the value of $X_m'/X_m$ increases beyond 1, so the curve from the new equation approaches logistic form. How can the effect of $X_m'/X_m$ on the shape of the growth curve be explained in biological terms?

Since $Xm'=(K+Sm)/a$ and $Xm=Sm/a$, the factor of K is entirely responsible for the value of $Xm'/Xm$. K is a Michaelis-Menten constant, which expresses the power of an organism to utilize a resource (in microbiology the 'affinity' of an organism for a particular nutrient). If K is small, the concentration of resource needed for a specific velocity approaching 0.5 Um is low, meaning that the organism has a low requirement for that particular resource (be it food in animals or different nutrients in plants). Growth is little affected by resource availability and population density will soon arrive at 0.9Xm. In this case, the value of $Xm'/Xm$ approaches 1.

However, when K is larger, growth will be more restricted by resource availability and a longer time will be required for population density to arrive at 0.9Xm. (Fig. 4)

## 4. METHODS OF DETERMINING PARAMETERS

Equation (5b) contains three parameters (Xm', Xm, Uc) and an initial population density (Xo). These parameters merit research since they are of considerable significance in ecology. We will describe two least square methods to determine these parameters, although other methods and refinement are possible.

(A) Using equation (5b), find a function Q1 for the sum of squares of errors between fitting and observed values, taking a set of paired values of $Uc\hat{t}(i)$ and $Uc\bar{t}(i)$, where i=1, 2,.....n.

$$Q_1 = \sum_{i=1}^{n} [\, U_c\hat{t} - U_c t \,]^2 = \sum_{i=1}^{n} [U_c(\hat{t}-t_o) - U_c(t-t_o)]^2$$

$$= \sum_{i=1}^{n} \left[ \left( \ln\frac{X}{X_o} - \ln\frac{X_m-X}{X_m-X_o} + \frac{X_m}{X_m'} \ln\frac{X_m-X}{X_m-X_o} \right) - U_c(t-t_o) \right]^2 \qquad (9a)$$

Let $\partial Q1/\partial Uc = 0$ and $\partial Q1/\partial Xm' = 0$, to obtain followins two equations:

$$U_c = \frac{\sum_{i=1}^{n} \left[ \left( \ln\frac{X}{X_o} - \ln\frac{X_m-X}{X_m-X_o} \right)(t-t_o) \right] + \frac{X_m}{X_m'} \sum_{i=1}^{n} \left[ \left( \ln\frac{X_m-X}{X_m-X_o} \right)(t-t_o) \right]}{\sum_{i=1}^{n} [\,(t-t_o)^2\,]} \qquad (9b)$$

$$U_c = \frac{\sum_{i=1}^{n} \left[ \left( \ln\frac{X}{X_o} - \ln\frac{X_m-X}{X_m-X_o} \right) \ln\frac{X_m-X}{X_m-X_o} \right] + \frac{X_m}{X_m'} \sum_{i=1}^{n} \left[ \ln\frac{X_m-X}{X_m-X_o} \right]^2}{\sum_{i=1}^{n} \left[ \left( \ln\frac{X_m-X}{X_m-X_o} \right)(t-t_o) \right]} \qquad (9c)$$

These two values of Uc (in equations 9b and 9c) are equal, therefore we can solve equations (9b) and (9c) for Xm'

$$X_m' =$$

$$\frac{X_m\left\{\sum_{i=1}^{n}\left[\left(\ln\frac{X_m-X}{X_m-X_o}\right)(t-t_o)\right]\right\}^2 - X_m\sum_{i=1}^{n}\left[(t-t_o)^2\right]\cdot\sum_{i=1}^{n}\left[\left(\ln\frac{X_m-X}{X_m-X_o}\right)^2\right]}{\sum_{i=1}^{n}\left[(t-t_o)^2\right]-\sum_{i=1}^{n}\left[\left(\ln\frac{X}{X_o}-\ln\frac{X_m-X}{X_m-X_o}\right)\ln\frac{X_m-X}{X_m-X_o}\right]-\sum_{i=1}^{n}\left[\left(\ln\frac{X}{X_o}-\ln\frac{X_m-X}{X_m-X_o}\right)(t-t_o)\right]\cdot\sum_{i=1}^{n}\left[\left(\ln\frac{X_m-X}{X_m-X_o}\right)(t-t_o)\right]} \qquad (9d)$$

Substituting a set of values X(i), t(i), and providing suitable values of Xm and Xo, we can obtain the value of Xm' possessing least square error. Then, we can obtain an optimised value of Uc by means of equation (9b) or (9c).

The problem is that we must have suitable estimates of Xm and Xo. Xm is the maximum value of population density, and can be derived from experience without difficulty. Xo, the starting population density, may be known explicitly, but if not it could be estimated by iterating equation (9a) with different values of Xo to minimise the error term.

(B) We could also use the least square method in equation (5a). In this case, we can obtain the least square estimates of Xm' and Uc without knowing the preliminary value Xo. The following equations will replace equations (9a), (9b), (9c), and (9d):

$$Q_e = \sum_{i=1}^{n}\left[\frac{dX}{dt}(1-X/X_m') - U_c X(1-X/X_m)\right]^2 \qquad (10a)$$

$$U_c = \frac{\sum_{i=1}^{n}\left[\frac{dX}{dt}\times\frac{dX}{dt}\right]-\frac{1}{X_m'}\sum_{i=1}^{n}\left[\frac{dX}{dt}X^2\frac{dX}{dt}\right]}{\sum\left[\frac{dX}{dt}X^2(1-X/X_m)\right]} \qquad (10b)$$

$$U_c = \frac{\sum_{i=1}^{n}\left[X\frac{dX}{dt}(1-X/X_m)\right]-\frac{1}{X_m'}\sum_{i=1}^{n}\frac{dX}{dt}X^2(1-X/X_m)\right]}{\sum_{i=1}^{n}\left[X(1-X/X_m)\right]^2} \qquad (10c)$$

$$X_m' = \frac{\sum\left[X\frac{dX}{dt}\right]^2\sum\left[X(1-X/X_m)\right]^2-\left\{\sum\left[X^2\frac{dX}{dt}\right](1-X/X_m)\right\}^2}{\sum\left[\left(\frac{dX}{dt}\right)^2X\right]\sum\left[X(1-X/X_m)\right]^2-\sum\left[X^2\frac{dX}{dt}(1-X/X_m)\right]\cdot\sum\left[X\frac{dX}{dt}(1-X/X_m)\right]} \qquad (10d)$$

However, the instantaneous values of dX/dt used in these equations are difficult to obtain, and inaccuracies may influence the derivation of parameters. Thus, we sussest using equation (9a), (9b), (9c), and (9d), but not (10a), (10b), (10c), and (10d).

Other methods of estimating parameters involve successive substitution in many of the previously used equations. But, these methods do not use least square estimation,

and therefore their results may be somewhat unsafe. However, they still have some value as a first approximation, or in checking the values estimated from the least square method.

## 5. APPLICATIONS OF THE BASIC MODEL

We wish to demonstrate the utility of our combined equation (5a and 5b) by concentrating on two typical problems in population biology.

### 5.1 Predicting the maximum value of population density

In a typical culture of microorganism (Fig. 6A), the population density, or time, at which the exponential phase gives way to decreasing growth, will depend on the initial supply of food in the medium. (Kitching, 1957)

Selecting data for two initial food concentrations (Table 4), it is apparent that any of the exponential ($\hat{t}$(1b)), logistic ($\hat{t}$(2b)) or combined ($\hat{t}$(5b)) equations can give a reasonable fit, although the error from the exponential equation is greater than from others. However, the predicted curves after 50 hours diverge considerably, and different maximum values of population density are obtained. Only the prediction from the combined equation matches the experimental observation (Fig. 6B).

TABLE 4. FITTING RESULTS OF MICROORGANISM GROWTH

| INITIAL CONCENTRATION 3% | | | | | INITIAL CONCENTRATION 0.5% | | | | |
|---|---|---|---|---|---|---|---|---|---|
| OBSERVED | | FITTED | | | OBSERVED | | FITTED | | |
| DENSITY (cells per c.c.) | t (hours) | $\hat{t}$(1b) (hours) | $\hat{t}$(2b) (hours) | $\hat{t}$(5b) (hours) | DENSITY (cells per c.c.) | t (hours) | $\hat{t}$(1b) (hours) | $\hat{t}$(2b) (hours) | $\hat{t}$(5b) (hours) |
| 132 | 1.5 | .47 | 1.5 | 1.5 | 132 | 1.5 | .53 | 1.5 | 1.5 |
| 148 | 2 | 1.10 | 2.06 | 2.06 | 148 | 2 | 1.16 | 2.06 | 2.07 |
| 234 | 4.5 | 3.60 | 4.29 | 4.32 | 234 | 4.5 | 3.70 | 4.32 | 4.35 |
| 316 | 6 | 5.24 | 5.75 | 5.80 | 316 | 6 | 5.36 | 5.80 | 5.84 |
| 661 | 9 | 9.28 | 9.35 | 9.43 | 661 | 9 | 9.45 | 9.45 | 9.52 |
| 891 | 11.5 | 10.91 | 10.81 | 10.90 | 891 | 11.5 | 11.10 | 10.92 | 11.01 |
| 1227 | 13 | 12.66 | 12.37 | 12.48 | 1227 | 13 | 12.88 | 12.51 | 12.61 |
| 1445 | 13.5 | 13.56 | 13.17 | 13.29 | 1445 | 13.5 | 13.78 | 13.33 | 13.43 |
| 2512 | 16.5 | 16.58 | 15.87 | 16.02 | 2512 | 16.5 | 16.84 | 16.10 | 16.22 |
| 3981 | 19 | 19.10 | 18.14 | 18.30 | 3981 | 19 | 19.39 | 18.43 | 18.56 |
| 5012 | 19.5 | 20.36 | 19.27 | 19.44 | 5012 | 19.5 | 20.67 | 19.61 | 19.74 |
| 6310 | 20 | 21.62 | 20.41 | 20.59 | 6310 | 20 | 21.95 | 20.81 | 20.93 |
| 6607 | 21.5 | 21.87 | 20.64 | 20.82 | 6607 | 21.5 | 22.2 | 21.05 | 21.17 |
| 11220 | 24 | 24.76 | 23.28 | 23.47 | 11220 | 24 | 25.13 | 23.88 | 23.97 |
| 15850 | 25.5 | 26.65 | 25.03 | 25.22 | 15850 | 25.5 | 27.05 | 25.82 | 25.87 |
| 25120 | 28 | 29.17 | 27.41 | 27.59 | 25120 | 28 | 29.60 | 28.61 | 28.55 |
| 44670 | 30.5 | 32.32 | 30.51 | 30.65 | 35050 | 31 | 31.44 | 30.87 | 30.70 |
| 75860 | 32.5 | 35.21 | 33.61 | 33.66 | 50100 | 34 | 33.42 | 33.76 | 33.43 |
| 125900 | 35.5 | 37.98 | 37.04 | 36.92 | 71000 | 37 | 35.35 | 37.68 | 37.38 |
| 199500 | 40 | 40.50 | 41.19 | 40.75 | 80000 | 40 | 36.01 | 39.64 | 39.89 |
| 251200 | 45 | 41.76 | 44.31 | 43.70 | | | | | |
| 305000 | 49 | 42.82 | 48.91 | 49.10 | | | | | |
| fitting parameters | | | | | | | | | |
| U ($hr^{-1}$) | | Ue=.18288 | U=.20543 | Uc=.20329 | | | Ue=.18056 | U=.20336 | Uc=.20126 |
| Xm(cells/c.c.) | | | 353000 | 325000 | | | | 108000 | 90000 |
| Xm'/Xm | | | | 3.2545 | | | | | 2.5037 |
| Xo(cells/c.c.) | | 132 | 132 | 132 | | | 132 | 132 | 132 |
| to(hr) | | .4713 | 1.5 | 1.5 | | | .5279 | 1.5 | 1.5 |
| fitting errors | | | | | | | | | |
| $\sqrt{\frac{\Sigma(\hat{t}-t)^2}{n-1}}$ | | 1.9 (hours) | 0.67 (hours) | 0.64 (hours) | | | 1.4 (hours) | 0.43 (hours) | 0.41 (hours) |
| R* | | .9897 | .9989 | .9989 | | | .9931 | .9994 | .9994 |
| P | | <.001 | <.001 | <.001 | | | <.001 | <.001 | <.001 |

R*---correlation coefficient between the observed value (t) and the fitted value($\hat{t}$).

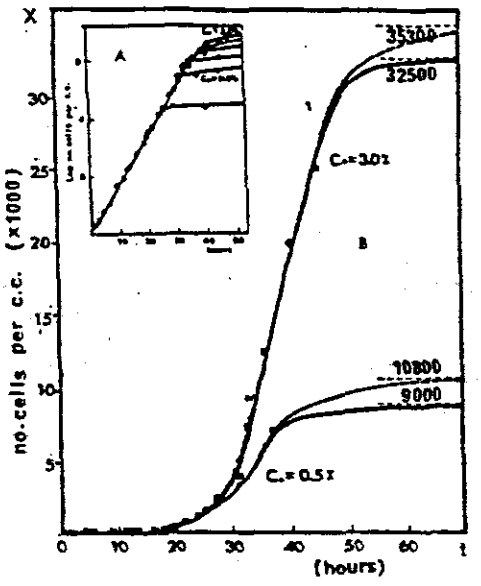


Fig. 6. Predicting curves of the maximum density of microorganism population. Data from Phelps (1936) and Rottier (1936) for axenic cultures of Tetrahymena (Glaucoma) pyriformis (=T.seleii). Curves are fitted to data before 50 hours (Table 4) and predicted to maximum population density. Observed maximum densities are 328800 cells per c.c. at 85 hours (for 3% yeast extract) and 89200 cells per c.c. at 73.5 hours (for 0.5% yeast extract) respectively.

——— from the combined equation ------from the logistic equation

5.2 Estimating the maximum velocity of population increment and the time at which the maximum velocity occurs

These factors are very important in forest management, and determine the time and amount of felling and thinning (Cui Qiwu et al., 1980a, 1980b).

Red pine (Pinus koraiensis Sieb. et Zucc.), a valuable commercial tree, possesses an unusual growth curve. Growth velocity continues increasing until the tree is close to its maximum biomass, and then diminishes very rapidly. Maximum velocity of wood volume increment often occurs after 70% of maximum wood volume has been achieved. This type of growth cannot be described by either the exponential or logistic equation, but a reasonable fit is obtained with the combined equation. The logistic equation estimates a maximum current annual increment (0.0338 $m^3 yr^{-1}$) occurring after 230 years, at a time when tree weight is half of its maximum. The combined equation estimates a maximum current annual increment (0.049 $m^3 yr^{-1}$) occurring after 242 years, at a time when tree weight is 70% of its maximum. The observed maximum increment is 0.055 $m^3 yr^{-1}$ occurring after 255 years, when tree weight is about 78% of its maximum.

It should be stressed that these data are from individual trees. An even age forest will display the same shape of growth curve, but the data may not apply to some natural forests. However, the pattern of population increase in a natural forest can be obtained by combining the growth curve for an individual tree with the known diameter composition of the forest. In general this diameter composition will often follow a normal distribution.

Beside this there is a senescence effect which complicates the influence of limiting resources. A second paper will deal with senescence and ensuing modifications to the combined equation should provide an even better fit than displayed in Fig. 7.

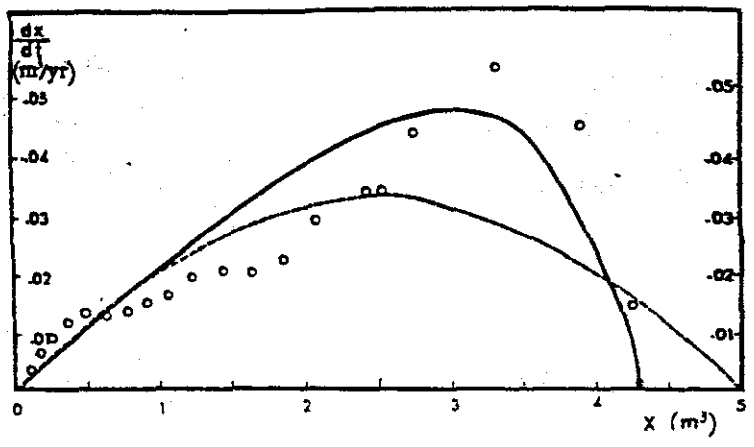


Fig. 7. Fitting curve of growth velocity of Red Pine

——— from the combined equation ------ from the logistic equation

$U_c$ = 0.0229963 year$^{-1}$ $U_L$ = 0.0270163 year$^{-1}$

$X_m$ = 4.31 m$^3$ $X_m'/X_m$ = 1.22231 $X_m$ = 5 m$^3$

$$\sqrt{\frac{\sum [\hat{t} - t]^2}{n-1}} = 7.9 \text{ years} \qquad \sqrt{\frac{\sum [\hat{t} - t]^2}{n-1}} = 9.5 \text{ years}$$

$R^* = 0.995$ $R^* = 0.992$

Conclusion:

The combined equation introduces a third term into the logistic equation, and it is therefore not surprising that better predictions of population growth will result. However this third term should not be viewed as a mere curve fitting device, since it appears to have genuine ecological significance through its ability to express the efficiency with which an organism can utilise a food or nutrient resource. We feel it has further potential application to various phenomena in ecology.

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# A NEW MODEL OF POPULATION INCREMENT WITH SEVERAL LIMITING CONDITIONS

Cui Qiwu and G. Lawson

## SUMMARY

A previous paper combined the exponential and logistic equations, with an attempt to describe the efficiency of resource utilisation, in a new general equation of single population growth. This paper incorporates two further limits to growth in the general equation:

(1) A death velocity parameter (D) is introduced, and is assumed proportional to population density (X) and $t^g$, where the exponent (g) expresses the life-span of the population;

(2) Seasonal periodicity is assumed to modify the population growth velocity parameter (Uc) according to a simple period function, $\sin^2(\pi t/12)$.

Therefore, we can rewrite the general equation as:

$$\frac{dX}{dt} = \frac{dX_1}{dt} - \frac{dX_2}{dt} = U_0 \sin^2(\pi t/12) X \frac{1 - X/X_m}{1 - X/X'_m} - D_0 X t^g$$

$$= U_c^* X \frac{1 - X/X_m^*}{1 - X/X'_m}$$

This form is identical in form to the previous general equation, but here

$$U_c^* = U_0 \sin^2(\pi t/12) - D_0 t^g$$

$$X_m^* = \frac{U_0 \sin^2(\pi t/12) - D_0 t^g}{U_0 \sin^2(\pi t/12) - X_m D_0 t^g / X'_m} X_m$$

Therefore this growth curve has a new velocity parameter of population increment and a new maximum population density. It also has a new inflexion point:

$$X_n^* = X'_m - \sqrt{X'^2_m - X_m^* X'_m}$$

The behaviour of the new equation is discussed, and in some circumstances it is shown to be very different to that of the classical logistic equation.

Key words: Ecological model, Population biology, Limiting resources, Biological kinetics

# 1. INTRODUCTION

In a previous paper (Cui & Lawson, 1982), we have derived a growth equation from the adsorption theory of chemical kinetics as follows:

$$\frac{dx}{dt} = U_c x \frac{1 - x/x_m}{1 - x/x_m'} \tag{1a}$$

where, X is population density at time t;
Xm is the maximum value of X, allowed by the limiting nutrient;
Xm'is a parameter concerning the efficiency of nutrient utilization by an organism;
Uc is a parameter concerning growth velocity.

This formula connects together the famous logistic and exponential equations, and is a reasonable model to explain the relationship between population increment and limiting nutrient supply. It can be reduced to the logistic equation when the value of Xm'/Xm is very large:

$$\frac{dx}{dt} = U_c x(1 - x/x_m) \tag{1b}$$

and to the exponential equation, ie

$$\frac{dx}{dt} = U_c x \ , \tag{1c}$$

when the value of Xm'/Xm nears 1.

Unfortunately, natural populations are complex and diverse in species. The increment of most populations is dependent not only on nutrient conditions, but also on factors such as water, heat and the age or vigor of component individuals. Thus equation (1a) is a considerable simplification; although it may completely describe some population increments, especially those of microorganisms growing in a culture medium. This paper seeks, therefore, to extend the applicability of the general equation by incorporating modifications to account for seasonal variation and senescence.

## 2. DEPENDENCE OF THE VELOCITY OF POPULATION INCREMENT ON SENESCENCE, DEATH, AND THE SEASONAL VARIATION OF CLIMATE

### 2.1 Death of component individuals in population and the dependence of death rate on population density

All populations, even microorganisms in exponential growth, eventually involve the simultaneous growth and death of component individuals. The velocity of population increment can be divided into two parts: one is its growth velocity (including the weight increase of component individuals and the formation of new component individuals) which can be expressed as dX1/dt, another is its death velocity (including also loss of weight of component individuals, as falling leaves of trees) which can be expressed as dX2/dt, ie

$$\frac{dx}{dt} = \frac{dx_1}{dt} - \frac{dx_2}{dt} \tag{2}$$

It is probably acceptable to assume that death velocity is proportional to population density at any particular instant, although it is possible to imagine that some dietary deficiencies in the past could affect present susceptibility to disease and therefore mortality. (Murdie, 1976.). Thus, we have:

$$\frac{dx_2}{dt} = Dx \tag{3a}$$

The first term in the right hand side of equation (2) should equal the right hand side of equation (1a), ie (further sophistications could account for possible time lags between conception and birth, but at the moment we do not consider that these are necessary.)

$$\frac{dx_1}{dt} = U_c x \frac{1 - x/x_m}{1 - x/x'_m} \tag{3b}$$

therefore, we can rewrite equation (2) as:

$$\frac{dx}{dt} = U_c x \frac{1 - x/x_m}{1 - x/x'_m} - Dx \tag{4a}$$

or

$$\frac{dx}{x\,dt} = U_c \frac{1 - x/x_m}{1 - x/x'_m} - D \tag{4b}$$

Fig. 1 and Fig. 2 express the relationships between growth velocity, death velocity and their combined results (called population incremental velocity).

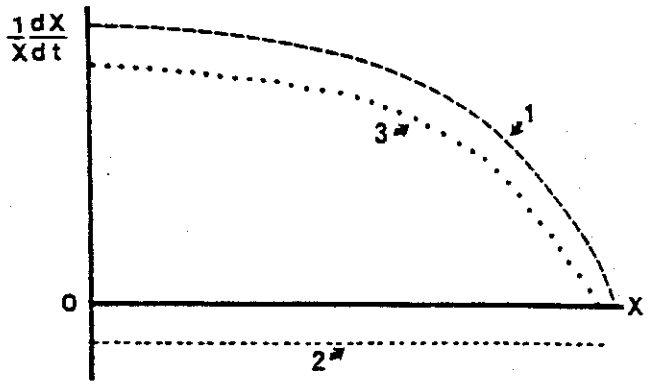



Fig. 1. Dependence of the specific velocity of population increment on population density

1. Specific growth velocity, Uc(1-X/Xm)/(1-X/Xm')
2. Specific death velocity, D
3. Combined result, dX/Xdt

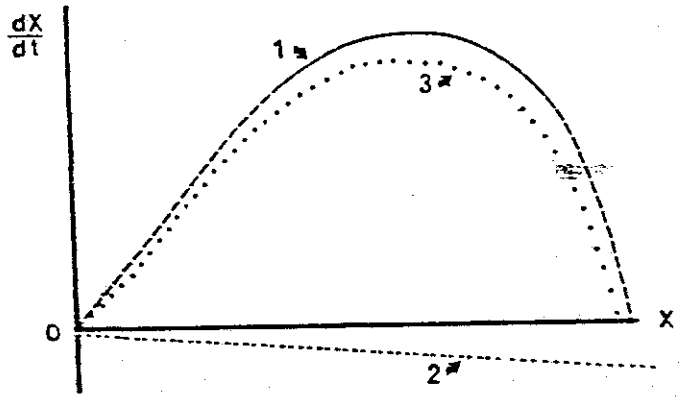


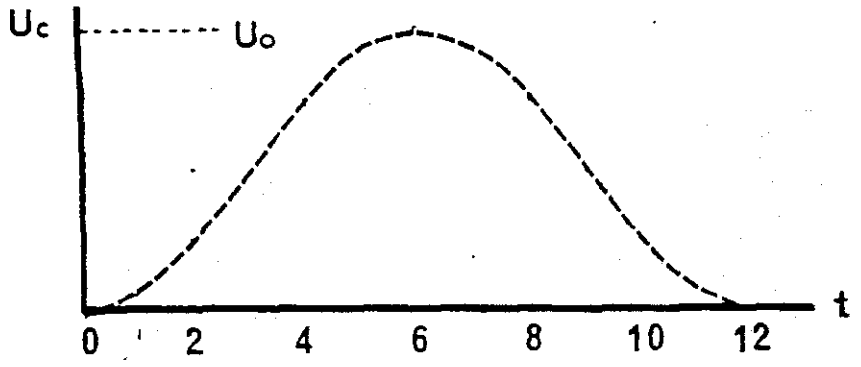

Fig. 2. Dependence of the velocity of population increment on population density

1. Growth velocity, UcX(1-X/Xm)/(1-X/Xm')
2. Death velocity, DX
3. Combined result, dX/dt

2.2 A simple expression of seasonal variation and the decrease of population visour

Plant populations have an obvious periodic variation over a year from spring to winter. This periodic variation is caused by various physiological processes within the plant itself which are trissered by a combination of environmental conditions such as temperature and day-lensth. However, isnorins the physiology of the plant, the seasonality of srowth is a simple conseauence of the fact that the earth moves around the sun with a period of 12 months. Thus we can use a simple time function to express the srowth velocity parameter Uc:

$$U_c(t) = U_o \sin^2(\pi t/12) \qquad (5a)$$




Fis. 3. Seasonal variation of srowth velocity parameter Uc(t)
(t in month)

Senescence is common to the development of all livins things. As the age of a population increases, the incremental velocity of the population will decrease, and component individuals will become old and feeble. This phenomenon is obvious in perennial plants (such as trees) and animal populations. It is possible to express this law with a simple time function usins a parameter for initial death velocity (Do), and an exponent, s, which expresses the life-span of the population, ie

$$D(t) = D_o t^s \qquad (5b)$$

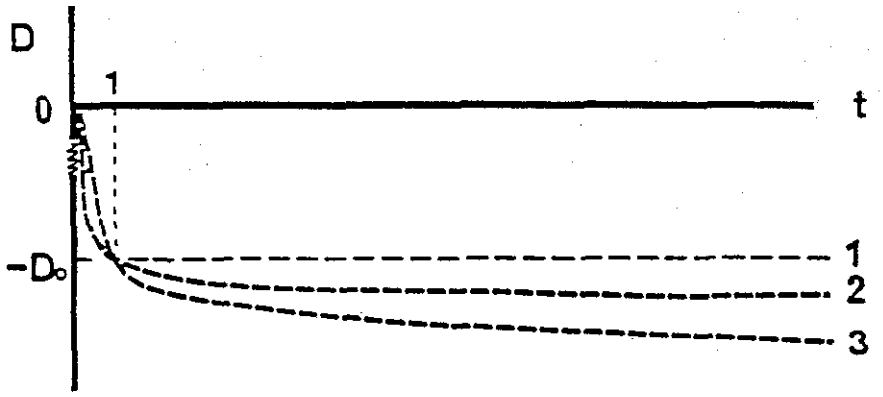



Fig. 4. Variation of death velocity parameter D(t) with time
Do is the initial value of D in the first month (t=1)

1. s=0
2. s=0.001
3. s=0.002

Therefore, equation (4a) and (4b) can be rewritten to include these amendments:

$$\frac{dX}{dt} = U_0 \sin^2(\pi t/12)\, X \frac{1 - X/X_m}{1 - X/X'_m} - D_0 t^s X \qquad (6a)$$

or

$$\frac{dX}{X\,dt} = U_0 \sin^2(\pi t/12) \frac{1 - X/X_m}{1 - X/X'_m} - D_0 t^s \qquad (6b)$$

Note: Uo and Do are in units of $month^{-2}$, whereas Uc and D in equation (4a or 4b) are in units of $time^{-1}$.

## 3. BEHAVIOUR OF THE NEW EQUATION AND THE BIOLOGICAL SIGNIFICANCE OF ITS PARAMETERS

To illustrate the similarities and differences between the new equation (6a) and the previous equation (1a), we will start to discuss from equation (4a).

### 3.1 A new maximum population density Xm*

The new maximum population Xm* can be obtained from the value of X in the right hand side of equation (4a) at dX/dt=0, ie

$$\frac{dx}{dt} = U_c x \frac{1 - x/x_m}{1 - x/x_m'} - Dx = 0 \qquad (7a)$$

$$x_m^* = \frac{1 - D/U_c}{1 - Dx_m/U_c x_m'} x_m \qquad (7b)$$

It is useful to consider the relationship between Xm (theoretical carrying capacity) and Xm* (maximum observed density). Fig. 5 shows how this relationship depends on the ratios of D/Uc and Xm/Xm'.

When D/Uc→0 or Xm/Xm'→1, then Xm*→Xm, otherwise the value of Xm* is always less than the value of Xm.

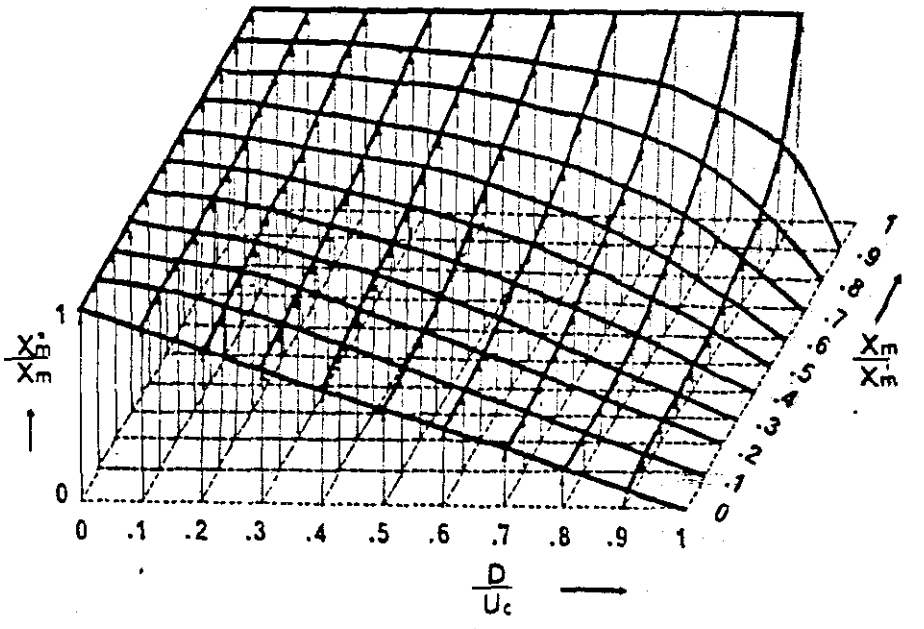



Fig. 5. Dependence of Xm*/Xm on the ratios of D/Uc and Xm/Xm'

In the case of microorganisms in continuous culture, population density can be maintained at a stable level which is dependant on the ratio of output rate or dilution rate (equivalent to D in equation (7b)) and specific growth rate (equivalent to Uc in equation (7b)). This phenomenon could be explained by equations (7a) and (7b), but not the exponential equation which is normally applied to microorganism growth. Likewise, over-mature forests (where D/Uc is large), and managed forests (where part of production is thinned or harvested, ie D>0) are not adequately described by the logistic equation. The introduction of a death term (D) into the new equation ensures that their maximum density is always less than the theoretical carrying capacity.

Fig. 5 also demonstrates that Xm/Xm' should be as close as possible to unity for maximum population density to approach the theoretical carrying capacity. This means that the efficiency with which food or nutrient can be utilised (Xm/Xm') influences not only the rate of population growth but also the eventual maximum population density.

3.2 A new velocity parameter Uc*

We can rewrite equation (4a) as follows:

$$\frac{dX}{dt} = U_c X \frac{1 - X/X_m}{1 - X/X_m'} - DX$$

$$= \frac{X_m'}{X_m} U_c X \left( \frac{X_m - X}{X_m' - X} - \frac{D X_m}{U_c X_m'} \right)$$

$$= \frac{X_m'}{X_m} U_c X \frac{X_m (1 - D/U_c) - X (1 - D X_m / U_c X_m')}{X_m' - X} \qquad (8a)$$

Using the relationship (7b) Xm*=Xm(1-D/Uc)/(1-DXm/UcXm'), then we have:

$$\frac{dX}{dt} = \frac{X_m'}{X_m} U_c X \frac{X_m^* - X}{X_m' - X} \left( 1 - \frac{D X_m}{U_c X_m'} \right)$$

$$= \frac{X_m'}{X_m^*} U_c X \frac{X_m^* - X}{X_m' - X} \left( 1 - \frac{D}{U_c} \right)$$

$$= U_c^* X \frac{1 - X/X_m^*}{1 - X/X_m'} \qquad (8b)$$

where Uc* is a new velocity parameter, and equals Uc-D

3.3 A new inflection point Xn* (at which growth rate begins to decrease)

By differentating equation (4a) again, and letting it equal zero, we have:

$$\frac{d(dX/dt)}{dX} = \frac{X_m' [(X_m - 2X)(X_m' - X) + X(X_m - X)] U_c}{X_m (X_m' - X)^2} - D = 0$$

$$X_n^* = \frac{(U_c X_m' - D X_m) X_m' - \sqrt{(U_c X_m' - D X_m)^2 X_m'^2 - (U_c X_m' - D X_m)(U_c - D) X_m X_m'^2}}{U_c X_m' - D X_m} \qquad (9a)$$

Using the relationship (7b) Xm*=Xm(1-D/Uc)/(1-DXm/UcXm') again, then we have:

$$\frac{X_n^*}{X_m'} = 1 - \sqrt{1 - \frac{X_m^*}{X_m'}}$$

or

$$\frac{X_n^*}{X_m^*} = \frac{X_m'}{X_m^*} - \sqrt{\left(\frac{X_m'}{X_m^*}\right)^2 - \frac{X_m'}{X_m^*}}$$

This form is very simple and is similar to that listed in the first paper (using here Xm* instead of Xm).

3.4 Behaviour of the new equation

The behaviour of equation (8b), with parameters Xm* and Uc*, is similar to the behaviour of the previous equation (1a) with the parameters Xm and Uc. Seasonal variation (5a) and senescence (5b) only modify the values of parameters Uc* and Xm*. Therefore, we can easily rewrite the new equation as follows:

$$\frac{dX}{X\,dt} = [U_o \sin^2(\pi t/12) - D_o t^g] \frac{1 - X/X_m^*}{1 - X/X'_m}$$

where

$$X_m^* = \frac{U_o \sin^2(\pi t/12) - D_o t^g}{U_o \sin^2(\pi t/12) - D_o t^g X_m / X'_m} X_m \qquad (10)$$

Equation (10) can be reduced to 24 simple forms in different circumstances, some of which are listed as follows:

A. $\frac{dX}{dt} = U_c X \frac{1 - X/X_m}{1 - X/X'_m}$ at $U_c(t) = U_c$, $D_o = 0$

this is the combined equation (1a);

B. $\frac{dX}{dt} = U_L X (1 - X/X_m)$ at $U_c(t) = U_L$, $D_o = 0$, $X'_m \gg X_m$

this is the logistic equation (1b);

C. $\frac{dX}{dt} = U_e X$ at $U_c(t) = U_e$, $D_o = 0$, $X'_m = X_m$

this is the exponential equation (1c);

The three above equations were introduced in the first paper.

D. $\frac{dX}{X\,dt} = U_L(1 - X/X_m) - D_o$ at $U_c(t) = U_L$, $D_o < 0.5U_o$, $g = 0$, $X'_m \gg X_m$

this form is often used in the literature.

E. $\frac{dX}{X\,dt} = (U_o - D_o)(1 - X/X_m^*)/(1 - X/X'_m)$ at $U_c(t) = U_c$, $D_o < 0.5U_o$, $g = 0$, $X'_m > X_m$

this form has been developed as equation (8b).

F. $$\frac{dx}{x\,dt} = U_0[\sin^2(\pi t/12) - 0.5]\frac{1 - x/x_m^*}{1 - x/x_m'} \qquad \text{at} \quad D_0 = 0.5U_0,\ g = 0$$

this is a stable period fluctuating function with the mean value Xo, which may be suitable for herbacedus perennials.

G. $$\frac{dx}{x\,dt} = U_0[\sin^2(\pi t/12) - 0.5t^g]\frac{1 - x/x_m^*}{1 - x/x_m'} \qquad \text{at} \quad D_0 = 0.5U_0$$

this is a period function with diminishing fluctuations;

H. $$\frac{dx}{x\,dt} = U_0\sin^2(\pi t/12)\frac{1 - x/x_m}{1 - x/x_m'} \qquad \text{at} \quad D_0 = 0$$

this is a S-shaped curve with diminishing fluctuations and a Xm-asymptote;

I. $$\frac{dx}{x\,dt} = [U_0\sin^2(\pi t/12) - D_0]\frac{1 - x/x_m^*}{1 - x/x_m'} \qquad \text{at} \quad D_0 < 0.5U_0,\ g = 0$$

this is a S-shaped curve with diminishing fluctuations;

J. $$\frac{dx}{x\,dt} = [U_0\sin^2(\pi t/12) - D_0t^g]\frac{1 - x/x_m^*}{1 - x/x_m'} \qquad \text{at} \quad D_0 < 0.5U_0,\ g > 0,\ x_m' > x_m$$

this is a common form of equation (10), which possesses following charactistics:

(a) population density increases along a S-curve to approach a maximum value, from which it subsequently decreases due to senescence;

(b) the whole life history is represented by a set of fluctuating waves with diminishing amplitudes.

## 4.CONCLUSION AND DISCUSSION----A FINAL COMMENT ON THE VERHULST-PEARL LOGISTIC EQUATION

The Verhulst-Pearl logistic equation (Verhulst, 1838; Pearl and Reed, 1920) has existed for over one hundred years. This equation has had great influence and continues to be used. Much experimental effort has been put into simulating the phases of population growth, particularly with microorganisms and insects. Reasonable fits to the logistic curve can be obtained provided that the right organism is chosen and the conditions are carefully defined (eg the growth of Paramecium in a limited volume of nutritive medium-Gause, 1934). However, even in such rarified experimental models, departures from the ideal curve of population growth are commoner than good conformity (Feller, 1940; Sang, 1950). Lag phases at the start of the exponential growth period and over-shooting of the theoretical Xm-asymptote are common, and the life cycles of most organisms involve periodicities of reproduction so that the growth of their populations occurs in steps or jumps rather than as a smooth curve.

Unfortunately, the logistic hypothesis remains central to population biology, although many variations have been derived, eg Gompertz, Von Bertalanffy, Mitscerlich, Weibull, Smith and so on. (Yanss, 1978; May, 1976) These variations emphasise departures from logistic equation only in forms, but not in essential aspects, and thus the basis on which the logistic equation was established has never been shaken. This paper, in addition the previous paper, tries to change the logistic hypothesis in principle. Using the adsorption theory of chemical kinetics as an analogue for resource utilization in organism populations, a new equation has been derived, which also includes the effects of death, season and ageing on population increment. This new equation behaves differently to the logistic equation, and can be used in a wide range of ecological situations, including populations of microorganism, annual and perennial plants, and perhaps also in the study of some animal populations. Its main characteristics can be summarized in following graph:

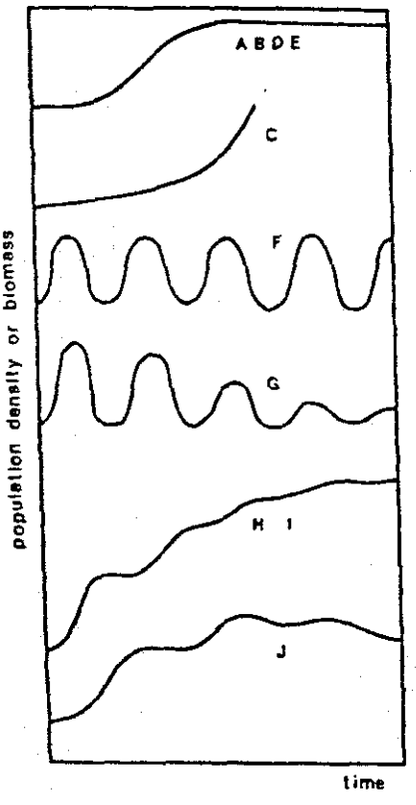



Fig. 6. Behaviour of the new equation
(see previous section for explanation of lettering)

The logistic curve is only accurate when the following conditions pertain:

$$K_m' \gg K_m \quad , \quad D_0 = 0 \quad , \quad U_i(t) = 0.5\,U_0$$

Therefore it is not surprising that single populations should frequently depart from the logistic assumption, and it is our hope that the new general equation given here can explain these departures, whilst remaining a theoretical and mechanistic tool, rather than a complicated curve-fitting device.

## ACKNOWLEDGMENTS

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# APPLICATION: CALCULATIONS OF THE CONTROL INDICES USED IN FOREST MANAGEMENT

Cui Qiwu

## SUMMARY

Using the new growth equation of single populations, which was derived by Cui and Lawson, and the 'chemostat system' theory used in semi-continuous culture of microorganism populations, this paper provides a new forest growth model and a number of control indices which can be used in forest management:

(1) Cutting intensity. In semi-continuous selected cutting of forest management, the cutting intensity is increased when the harvested cycle period is decreased. The maximum cutting intensity will be obtained in the completely continuous selected cutting. Therefore 'diligent cutting' or 'slight cutting' should be encouraged.

(2) Productivity. In the completely continuous selected cutting, the productivity curve follows the growth curve. The maximum productivity occurs at the inflexion point usually beyond 0.5Xm (half the maximum population density). In the semi-continuous selected cutting, productivity can be calculated from the index of IRP.

(3) Stable state. When the cutting intensity is less than the incremental velocity parameter (D < Uc), forest population density can approach a stable state. Its value is not only dependent on the parameters of the growth curve, but is also dependent on the cutting method.

Key words: Forest management, Population model, Ecological balance

## 1. INTRODUCTION

Three years ago, the author derived a mathematical model of forest management for sustained yield (Cui et al., 1980). The model described the growth of a forest population under the condition that a part was harvested in a cycle with fixed period. This is a type of event model describing the changes in a population subject to sudden, more or less catastrophic, events. The population density falls rapidly during a short period, then recovers to approach its original level according to a normal growth rate after the event has happened. The questions to be answered by the model are how the population can be maintained and how its stable state depends on the parameters of the growth curve and the event's behaviour.

These models were originally derived in order to determine the influence of changing dilution rate on the output rate of population in the semi-continuous culture of microorganisms (Monod, 1950). The same arguments, however, apply to other circumstances such as studying the effect of hydraulic conditions on the numbers of bottom-dwelling species (Smith, 1982), and the intermittent release of toxins. the models of harvested populations used in fisheries (Schaefer, 1954; Pella and Tomlinson, 1969; May, 1981) are merely special cases (ie continuous harvests). For different uses the basic growth equations on which the event models are established are different. The exponential equation, as the basic growth equation, is usually used in semi-continuous culture of microorganisms. The logistic equations are used in author's paper and Smith's paper. The results obtained from the event models are different when these different basic growth equations are used. For example, with the logistic equation, a maximum rate of growth occurs at half the carrying capacity. Therefore the maximum harvest, at the ideal centre point, from the model of the forest management which is established on the basic logistic equation, is also at half the carrying capacity. The situation seems not to agree with that in practice. Therefore the harvest at the non-ideal centre point was discussed, and control indices under conditions of the non-maximum harvest were calculated in that paper.

In the present paper, we wish to discuss the use of the new equation, which was derived by Cui and Lawson (1982). This is shown as equation 1a.

$$\frac{dx}{dt} = U_c x \frac{1 - x/x_m}{1 - x/x'_m} - Dx = U_c^* x \frac{1 - x/x_m^*}{1 - x/x'_m} \qquad (1a)$$

If we use equation (1a) as the basic equation instead of the logistic equation for the model of forest management , this then establishes another new management model instead of the one discussed previously. Where Xm is carrying capacity; Uc, D are the growth and death velocity parameters respectively; and

$$U_c^* = U_c - D \quad , \quad x_m^* = \frac{U_c - D}{U_c - Dx_m/x'_m} x_m$$

are the increment velocity parameters and the maximum population density in practice respectively, when the death velocity parameter is considered. If Xm/X'm=0, equation (1a) can be reduced to the following form usual in the literature:

$$\frac{dx}{dt} = U_c x (1 - x/x_m) - Dx \qquad (1b)$$

However, under more general conditions, $X_m/X'_m \neq 0$, and the behaviour of the equation is then dependent on the value of $X_m/X'_m$.

$X_m/X'_m$ represent the efficiency of nutrient utilization by an organism. Its value is between 0 and 1. With ratios approaching unity the efficiency is high; Lower ratios indicate that population increment is quickly restricted by limiting resources. $X'_m$, as the third parameter, is introduced into the logistic equation. This is not only as a curve fitting device, since it appears to have genuine ecological significance through its ability to express the efficiency with which an organism can utilise a food or nutrient resource. Using this new equation as a basic growth equation, the model of forest management will have many new characteristics. In particular, the ideal centre point will be moved to the right hand side of the middle point of the growth curve, ie at the point beyond $0.5X_m$. This result is acceptable to foresters, and generally agrees with the data in practice.

As shown in the discussions in an earlier paper, in the species case ($X_m/X'_m=0$), the new equation (1a) can be reduced to the logistic form (1b), and the new model of the forest management in the present paper will be also reduced to the model which was derived by the author three years ago.

## 2. THE GENERAL FORM OF THE FOREST MANAGEMENT MODEL AND THE HARVESTED CYCLE PERIOD

We can rewrite equation (1a) in its integral form:

$$\ln \frac{X_2}{X_1} - \ln \frac{X_m^* - X_2}{X_m^* - X_1} + \frac{X_m^*}{X_m'} \ln \frac{X_m^* - X_2}{X_m^* - X_1} = U_c^*(t_2 - t_1) = U_c^* \Delta t \qquad (2a)$$

where $t_1$ and $t_2$ are times at two points on the integral curve respectively; $X_1$ and $X_2$ are the population densitites at the respective points. Population density varies with time as curve 1 in Fig. 1.

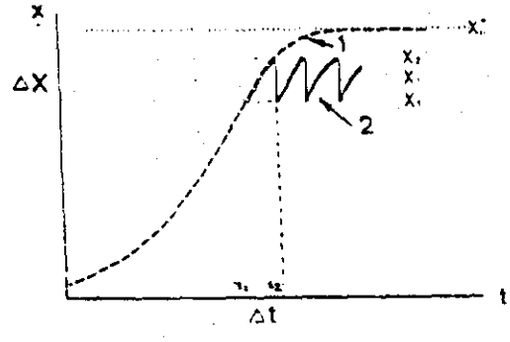


Fig. 1. Population density varies with time

------ natural forest population
——— managed forest population

It is also an S-shaped growth curve, but not symmetrical and its inflexion point is not at $0.5X_m^*$. The position of the inflexion and the asymmetric relation are dependent on the quotient $X_m^*/X_m'$. Curve 1 is usually used for a natural population in a closed system. In this system, neither input nor output of nutrients takes place, ie $X_m^*$ is a constant. For a managed forest, the model applies if the nutrient which is carried out with the wood harvested can be replenished in another way, ie the net transfer of nutrients is zero. This case resembles that of the 'chemostat system' in the semi-continuous culture of microorganism.

We would like to discuss the model of forest management under the following conditions:

(1) Selective cutting: in which only a proportion of the old trees are cut and all young trees are retained. In this case, the forest environment has not been destroyed. After cutting, therefore, the forest still grows according to the original law, but the population density is decreased, from $X_2$ (the population density before cutting) to $X_1$ (the population density after cutting; see curve 2 in Fig. 1).

(2) Stable state: This is to be cut again when the population density returns to the point $X_2$. We can consider it as a system to which the amount of forest growth during the period $(t_2 - t_1 = \Delta t)$ is added and from which the cutting wood is taken away semi-continuously, and the two parts (input and output) are equal in amount. The system can be maintained in a dynamic equilibrium state.

Curve 2 in Fig. 1 describes the behaviour of this system. Let us use $\alpha$ to express the cutting ratio during the period $(t_2 - t_1)$, ie

$$\alpha = \frac{X_2 - X_1}{X_2} = \frac{\Delta X}{X_2}$$

Taking the middle point Xi between $X_1$ and $X_2$, we have:

$$X_2 = X_i + 0.5\Delta X = X_i + 0.5\alpha X_2$$
$$X_2 = X_i/(1 - 0.5\alpha) \qquad (2b)$$

and
$$X_1 = X_i - 0.5\Delta X = X_i - 0.5\alpha X_2 = (1-\alpha)X_i/(1-0.5\alpha)$$

Using ratios $\beta = Xi/Xm$, and substituting equation (2b) into equation (2a), we have:

$$\Delta t = \frac{1}{U_c^*}\left[\ln\frac{1}{1-\alpha} - \left(1 - \frac{X_m^*}{X_m'}\right)\ln\frac{1-\beta-0.5\alpha}{1-\beta-0.5\alpha+\alpha\beta}\right]$$
$$= \frac{1}{U_c^*}\left(1 - \frac{X_m^*}{X_m'}\right)\ln\frac{1-\beta-0.5\alpha+\alpha\beta}{(1-\beta-0.5\alpha)(1-\alpha)^{1/(1-X_m^*/X_m')}} \qquad (2c)$$

This equation describes the harvested cycle period ($\Delta t$), which is needed to maintain a steady state, is a function of the cutting ratio ($\alpha$), the relative cutting position ($\beta$) and the parameters of the growth curve ($X^*_m/X'_m$, $U_c$). For a particular population, the parameters are constants, the equation (2c) therefore can be used in the study of control indices used in forest management, ie the relationship among $\alpha$, $\beta$ and $\Delta t$. An index of relative cycle period (IRCP) can be constructed to express the relationship between $\alpha$, $\beta$, $X^*_m/X'_m$ and $\Delta t$:

$$IRCP = U_c^* \Delta t$$

Table 1 in the addenda lists a set of values under different conditions.

## 3. CUTTING INTENSITY

For cutting at the middle point ($\beta = 0.5$), we can obtain a simple form of equation (2c):

$$\Delta t_{0.5} = \frac{1}{U_c^*}\left(1 - \frac{X_m^*}{X'_m}\right) \ln \frac{1}{(1-\alpha)^{1+1/(1-X_m^*/X'_m)}}$$

$$= \frac{1}{U_c^*}\left(2 - \frac{X_m^*}{X'_m}\right) \ln \frac{1}{1-\alpha}$$

or

$$\alpha_{0.5} = 1 - \exp\left[\frac{-U_c^* \Delta t}{2 - X_m^*/X'_m}\right] \qquad (3a)$$

The cutting ratio in unit time, $\alpha/\Delta t$, is called the cutting intensity which is a useful index for comparing the harvests between different cutting methods. At the middle point, we have $D^*_{0.5}$

$$D^*_{0.5} = \left[\frac{\alpha}{\Delta t}\right]_{0.5} = \frac{1 - \exp[-U_c^* \Delta t/(2 - X_m^*/X'_m)]}{\Delta t} \qquad (3b)$$

Fig. 2 shows the relationship between $\Delta t$ and $D^*_{0.5}$

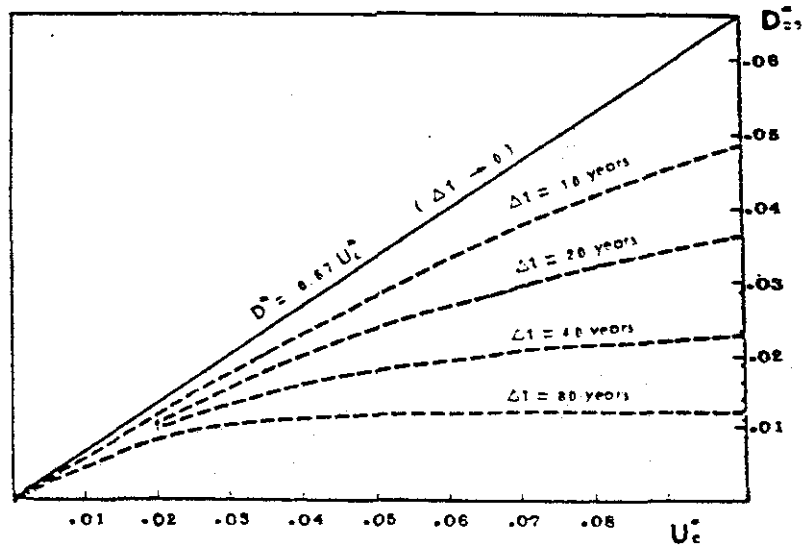


Fig. 2. Cutting indensity varies with the harvested cycle period

For an extreme case, ie $\Delta t=0$ called continuous selective cutting (to be cut point by point during an extreme short period), we can use Robieda's law to obtain: (differentiating numerator and denominator simultaneously)

$$\lim_{\Delta t \to 0} D^*_{0.5} = \lim_{\Delta t \to 0} \frac{0 - \exp[-U_c^* \Delta t/(2 - X_m^*/X_m')] \cdot [-U_c^*/(2 - X_m^*/X_m')]}{1}$$

$$= \frac{U_c^*}{2 - X_m^*/X_m'} \qquad (3c)$$

(note: when $X_m^*/X_m' \to 0$, $D^*_{0.5} \to 0.5U_c^*$, this relationship was obtained in the previous paper (Cui et al., 1980)).

Equation (3c) is only used for the middle point, ie at $\beta = 0.5$. For general situations, an expanded form of lim $D^*$ will be obtained as follows: (from equation (2c))

$$\lim_{\Delta t \to 0} D^* = \lim_{\Delta t \to 0} \frac{d}{\Delta t} = \frac{(1-\beta) U_c^*}{1 - \beta X_m^*/X_m'} \qquad (3d)$$

Equation (3d) expressed the upper limitations of cutting intensity (continuous selective cutting, ie $\Delta t \to 0$). Its value is only dependent on the parameters of the growth curve ($X_m^*/X_m'$, $U_c^*$) and the relative cutting position ($\beta$). However, in general, cutting intensity is less than these values and is also dependent on the harvested cycle period ($\Delta t$), when $\Delta t$ is not equal to zero. Although the relationship which is shown in Fig. 2 is merely for the middle point ($\beta=0.5$), but it is also similar (at least qualitatively) to the relationship between $D^*$ and $\Delta t$ under general conditions (ie $\beta \neq 0.5$). That is: the smaller the $\Delta t$, the larger the cutting intensity $D^*$. Therefore, 'diligent cutting ($\Delta t$ small)' or 'slisht cutting' should be encourased in forest management. In this case, a bigger harvest could be obtained when other conditions are the same. This reasoning is similar to that relating to semi-culture approaches to continuous culture in the production of microorganism populations: the output of the populations is increased when the cycle period ($\Delta t$) is decreased, and

the maximum output will be obtained in the completely continuous culture ($\Delta t' \to 0$). When $\Delta t \neq 0$ and $\beta \neq 0.5$, we have the following relationship instead of equation (3b) and (3d):

$$D^* = \frac{\partial}{\Delta t} = \frac{\partial U_c^*}{\left(1 - \frac{X_m^*}{X_m'}\right) \ln \frac{1 - \beta - 0.5\partial + \partial\beta}{(1-\beta-0.5\partial)(1-\partial)^{1/(1 - X_m^*/X_m')}}} \tag{3e}$$

An index of relative cutting intensity (IRCI) can be constructed to express the relationship between $X_m^*/X_m'$, $\partial$, $\beta$ and D

$$IRCI = D^*/U_c^*$$

Table 2 in the addenda lists a set of values under different conditions.

## 4. PRODUCTIVITY

Equation (3d) shows that: the smaller the value of $\beta$, the larger the cutting intensity. However, this has not expressed the relationship between productivity and $\beta$. Productivity, or harvest in unit time, is equal to $D^* X_2$. When $\beta$ is small, the value of $X_2$ is also small ($X_2 = Xi/(1-0.5\partial) = \beta X_m^*/(1-0.5\partial)$), although the value of $D^*$ is large. Therefore, productivity is dependent on $\beta$ in double times. Using $D^* X_2 / U_c^* X_m^*$ as an index of relative productivity (IRP), and from equation (2b) and (3e), we have

$$\frac{D^* X_2}{U_c^* X_m^*} = \frac{\partial}{\left(1 - \frac{X_m^*}{X_m'}\right) \ln \frac{1 - \beta - 0.5\partial + \partial\beta}{(1-\beta-0.5\partial)(1-\partial)^{1/(1 - X_m^*/X_m')}}} \cdot \frac{\beta}{1 - 0.5\partial} \tag{4a}$$

Table 3 in the addenda lists the relationship (4a) between relative productivity and $\partial$, $\beta$, $X_m^*/X_m'$ under general conditions. These control indices can be used in forest management.

When $\Delta t \to 0$, ie continuous selective cutting, equation (4a) can be reduced to the following equation according to the Robeida's law:

$$\lim_{\Delta t \to 0} \frac{D^* X_2}{U_c^* X_m^*} = \frac{\beta(1-\beta)}{1 - \beta X_m^*/X_m'} \tag{4b}$$

or

$$\lim_{\Delta t \to 0} \frac{D^* X_2}{U_c^* X_m^*} = \frac{D^*(U_c^* - D^*)}{U_c^* - D^* X_m^*/X_m'} \tag{4c}$$

Fig. 3 shows the relationship between the index of relative productivity (IRP) and the relative cutting position ($\beta$) under the condition of the continuous selective cutting (taking $X_m^*/X_m' = 0.8$).

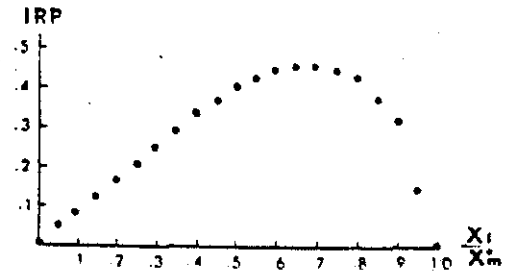


Fig. 3. Productivity distribution curve

Differentiating equation (4b), and letting it be equal to zero, we find the position where the maximum productivity occurs under the condition of continuous selective cuttings.

$$\frac{\partial}{\partial \beta}\left[\frac{\beta(1-\beta)}{1-\beta X_m^*/X_m'}\right] = 0$$

$$(1-2\beta)(1-\beta X_m^*/X_m') + \beta(1-\beta) X_m^*/X_m' = 0$$

$$\beta_n = X_m'/X_m^* - \sqrt{(X_m'/X_m^*)^2 - X_m'/X_m^*} \qquad (4d)$$

This relationship can also be obtained immediately from equation (1a): on that S-shaped growth curve a maximum increment velocity $(dX/dt)_m$ will occur at the inflexion point (Xn), and the relative position of the inflexion is at:

$$\frac{X_n^*}{X_m^*} = \frac{X_m'}{X_m^*} - \sqrt{\left(\frac{X_m'}{X_m^*}\right)^2 - \frac{X_m'}{X_m^*}} \qquad (4e)$$

In other words, the position where the maximum increment velocity occurs and the position where the maximum productivity is obtained are the same place, ie

$$(4d) = (4e) \quad , \quad or \quad \beta_n = X_n^*/X_m^*$$

The maximum relative productivity $(IRP)_m$ can be calculated as

$$\lim_{\Delta t \to 0}\left[\frac{D^* X_i}{U_i^* X_m^*}\right]_m = \frac{\beta_n(1-\beta_n)}{1-\beta_n X_m^*/X_m'}$$

$$= \left[X_m'/X_m^* - \sqrt{(X_m'/X_m^*)^2 - X_m'/X_m^*}\right]^2 \qquad (4f)$$

This shows that the maximum productivity in continuous selective cutting is only dependent on the parameters of the growth curve.

## 5. STABLE STATE

From equation (2c), we can solve for the relative cutting position ($\beta$), ie

$$\beta = \frac{0.5 D^* \Delta t - 1 + (1 - 0.5 D^* \Delta t)(1 - D^* \Delta t)^{1/(1 - x_m^*/x_m')} \exp[U_c^* \Delta t/(1 - x_m^*/x_m')]}{D^* \Delta t - 1 + (1 - D^* \Delta t)^{1/(1 - x_m^*/x_m')} \exp[U_c^* \Delta t/(1 - x_m^*/x_m')]} \tag{5a}$$

In the extreme case ($\Delta t \to 0$), we have:

$$\lim_{\Delta t \to 0} \beta = \frac{U_c^* - D^*}{U_c^* - D^* x_m^*/x_m'} \tag{5b}$$

$\beta$ can therefore indicate the position of a stable state maintained under conditions of different cutting intensity.

Equation (5a) and (5b) are used in general selective cutting and continuous selective cutting respectively. They show the stable state is not only dependent on the parameters ($X_m^*/X_m'$, $U_c^*$) of the growth curve, but is also dependent on the management method (expressed by $D^*$ and $\Delta t$). Fig. 4 shows the relationship between $\beta$ and $D^*/U_c^*$ or $X_m^*/X_m'$ under the condition of continuous selective cutting.

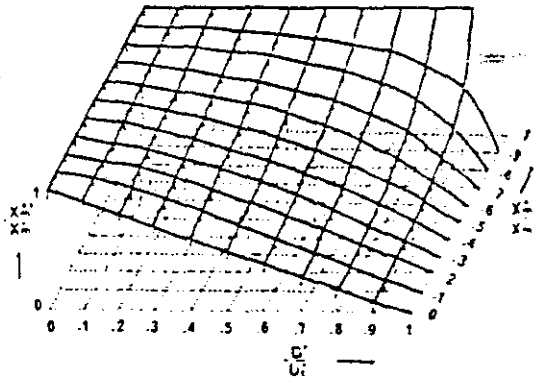

Fig. 4. Steady population density varies with the parameters of growth curve and the cutting method

Therefore for the general situations ie when $\Delta t$ does not approach zero, the position of the stable state will be lower than that expressed in Fig. 4. Although Fig. 4 and equation (5b) are only true for continuous selective cutting, they however have a theoretical value. We would like to analyse them another way.

Under the condition of management, population increment will follow the equation:

$$\frac{dx}{dt} = U_c^* x \frac{1 - x/x_m^*}{1 - x/x_m'} - D^* x \tag{6a}$$

The first term in the right hand side expresses the increment velocity of a population under natural conditions, the second term in the right hand side is the decreased velocity of the population due to cutting. If the first term is larger than the second term, then the population still increases, ie dX/dt > 0. This shows that there is a new incremental curve and which can be expressed as follows:

$$\frac{dx}{dt} = U_c^* x \frac{1 - x/x_m^*}{1 - x/x_m'} - D^* x = U_c^{**} x \frac{1 - x/x_m^{**}}{1 - x/x_m'}$$

where $$U_c^{**} = U_c^* - D^* \quad , \quad x_m^{**} = x_m^* (U_c^* - D^*)/(U_c^* - D^* x_m^*/x_m') \tag{6b}$$

This is still an S-shaped growth curve, but in this case a new incremental velocity parameter $U_c^{**}$ and a new maximum population density $X_m^{**}$ are included. Note that the value of the new maximum population density $X_m^{**}$ is equal to the value of the population density at the stable state as expressed in equation (5b). In other words, at the start if the incremental velocity in the natural state is larger than the cutting velocity, then population density will still increase. However, the amount of increment will vary with the population density as expressed in curve 1 in Fig. 5, and ultimately the population density will certainly approach a stable state. In that case, the first term and the second term in the right hand side of equation (6a) will become equal, then dX/dt=0.

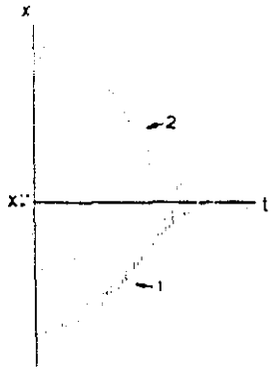


Fig. 5. Population density varies with time (in a managed forest population with a fixed cutting ratio).

Under another condition, ie if at the start the incremental velocity in the natural condition is less than the cutting velocity, then the population density will decrease, but the amount of decrease varies with population density as expressed in curve 2 in Fig. 5.

It should be pointed out that under the two conditions above, the population density will approach a stable state which is only dependent on the parameters of the growth curve ($X_m^*$, $X_m'$, $U_c^*$) and the cutting method (expressed by $D^*$ and $\Delta t$). When $D^* > U_c^*$ the population density at stable state approaches to zero. That means the forest population will be cut out completely.

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## ADDENDA

(A) TABLES AND EXAMPLES:

TABLE 1 INDICES OF RELATIVE CYCLE PERIOD ( IRCP )

| $x_m^*/x_m$ \ $\alpha$ (cutting ratio; %) | | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 |
|---|---|---|---|---|---|---|---|---|---|---|
| 0.0 | 0.1 | 0.12 | 0.25 | 0.40 | 0.57 | 0.77 | 1.01 | 1.32 | 1.76 | 2.48 |
| | 0.2 | 0.13 | 0.28 | 0.44 | 0.64 | 0.86 | 1.13 | 1.47 | 1.95 | 2.72 |
| | 0.3 | 0.15 | 0.32 | 0.51 | 0.73 | 0.98 | 1.29 | 1.67 | 2.20 | 3.03 |
| | 0.4 | 0.18 | 0.37 | 0.59 | 0.85 | 1.15 | 1.50 | 1.96 | 2.56 | 3.53 |
| | 0.5 | 0.21 | 0.45 | 0.71 | 1.02 | 1.39 | 1.83 | 2.41 | 3.22 | 4.61 |
| | 0.6 | 0.26 | 0.56 | 0.90 | 1.30 | 1.79 | 2.44 | 3.44 | 1.82 | / |
| | 0.7 | 0.35 | 0.75 | 1.23 | 1.85 | 2.77 | 17.4 | / | / | / |
| | 0.8 | 0.53 | 1.18 | 2.11 | / | / | / | / | / | / |
| | 0.9 | 1.13 | 1.58 | / | / | / | / | / | / | / |
| 0.2 | 0.1 | 0.11 | 0.24 | 0.39 | 0.56 | 0.75 | 0.99 | 1.30 | 1.73 | 2.45 |
| | 0.2 | 0.13 | 0.27 | 0.43 | 0.61 | 0.83 | 1.09 | 1.42 | 1.88 | 2.63 |
| | 0.3 | 0.14 | 0.30 | 0.48 | 0.68 | 0.92 | 1.21 | 1.58 | 2.08 | 2.89 |
| | 0.4 | 0.16 | 0.34 | 0.55 | 0.78 | 1.05 | 1.39 | 1.81 | 2.37 | 3.28 |
| | 0.5 | 0.19 | 0.40 | 0.64 | 0.92 | 1.25 | 1.65 | 2.17 | 2.90 | 4.14 |
| | 0.6 | 0.23 | 0.49 | 0.79 | 1.14 | 1.57 | 2.14 | 3.00 | 14.9 | / |
| | 0.7 | 0.30 | 0.65 | 1.06 | 1.58 | 2.36 | 14.1 | / | / | / |
| | 0.8 | 0.45 | 0.99 | 1.76 | / | / | / | / | / | / |
| | 0.9 | 0.93 | 12.7 | / | / | / | / | / | / | / |
| 0.4 | 0.1 | 0.11 | 0.24 | 0.38 | 0.54 | 0.74 | 0.97 | 1.28 | 1.70 | 2.41 |
| | 0.2 | 0.12 | 0.26 | 0.41 | 0.59 | 0.79 | 1.05 | 1.37 | 1.81 | 2.55 |
| | 0.3 | 0.13 | 0.28 | 0.45 | 0.64 | 0.87 | 1.14 | 1.49 | 1.96 | 2.74 |
| | 0.4 | 0.15 | 0.31 | 0.50 | 0.71 | 0.96 | 1.27 | 1.65 | 2.18 | 3.04 |
| | 0.5 | 0.17 | 0.36 | 0.57 | 0.82 | 1.11 | 1.47 | 1.93 | 2.58 | 3.68 |
| | 0.6 | 0.20 | 0.43 | 0.68 | 0.98 | 1.35 | 1.83 | 2.55 | 11.6 | / |
| | 0.7 | 0.25 | 0.54 | 0.88 | 1.31 | 1.94 | 10.8 | / | / | / |
| | 0.8 | 0.36 | 0.80 | 1.41 | / | / | / | / | / | / |
| | 0.9 | 0.72 | 9.59 | / | / | / | / | / | / | / |
| 0.6 | 0.1 | 0.11 | 0.23 | 0.37 | 0.53 | 0.72 | 0.95 | 1.25 | 1.67 | 2.38 |
| | 0.2 | 0.12 | 0.25 | 0.39 | 0.56 | 0.76 | 1.00 | 1.31 | 1.74 | 2.47 |
| | 0.3 | 0.12 | 0.26 | 0.42 | 0.60 | 0.81 | 1.06 | 1.39 | 1.84 | 2.60 |
| | 0.4 | 0.13 | 0.28 | 0.45 | 0.65 | 0.87 | 1.15 | 1.50 | 1.99 | 2.79 |
| | 0.5 | 0.15 | 0.31 | 0.50 | 0.72 | 0.97 | 1.28 | 1.69 | 2.25 | 3.22 |
| | 0.6 | 0.17 | 0.36 | 0.57 | 0.83 | 1.13 | 1.53 | 2.10 | 8.25 | / |
| | 0.7 | 0.20 | 0.44 | 0.71 | 1.04 | 1.52 | 7.50 | / | / | / |
| | 0.8 | 0.28 | 0.61 | 1.06 | / | / | / | / | / | / |
| | 0.9 | 0.52 | 6.47 | / | / | / | / | / | / | / |
| 0.8 | 0.1 | 0.11 | 0.22 | 0.36 | 0.52 | 0.71 | 0.94 | 1.23 | 1.64 | 2.34 |
| | 0.2 | 0.11 | 0.23 | 0.37 | 0.54 | 0.73 | 0.96 | 1.26 | 1.67 | 2.39 |
| | 0.3 | 0.11 | 0.24 | 0.39 | 0.55 | 0.75 | 0.99 | 1.30 | 1.73 | 2.45 |
| | 0.4 | 0.12 | 0.25 | 0.40 | 0.58 | 0.78 | 1.03 | 1.35 | 1.80 | 2.54 |
| | 0.5 | 0.13 | 0.27 | 0.43 | 0.61 | 0.83 | 1.10 | 1.44 | 1.93 | 2.76 |
| | 0.6 | 0.14 | 0.29 | 0.47 | 0.67 | 0.91 | 1.22 | 1.65 | 4.93 | / |
| | 0.7 | 0.15 | 0.33 | 0.53 | 0.78 | 1.11 | 4.21 | / | / | / |
| | 0.8 | 0.19 | 0.41 | 0.71 | / | / | / | / | / | / |
| | 0.9 | 0.31 | 3.35 | / | / | / | / | / | / | / |

TABLE 2 INDICES OF RELATIVE CUTTING INTENSITY ( IRCI )

| $x_m^+/x_m^-$ | β \ ∂ IRCI | ∂ (cutting ratio; %) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 |
| 0.0 | 0.1 | 0.85 | 0.81 | 0.76 | 0.71 | 0.65 | 0.59 | 0.53 | 0.46 | 0.36 |
| | 0.2 | 0.76 | 0.72 | 0.67 | 0.63 | 0.58 | 0.53 | 0.47 | 0.41 | 0.33 |
| | 0.3 | 0.66 | 0.63 | 0.59 | 0.55 | 0.51 | 0.47 | 0.42 | 0.36 | 0.30 |
| | 0.4 | 0.57 | 0.54 | 0.51 | 0.47 | 0.44 | 0.40 | 0.36 | 0.31 | 0.26 |
| | 0.5 | 0.47 | 0.45 | 0.42 | 0.39 | 0.36 | 0.33 | 0.29 | 0.25 | 0.20 |
| | 0.6 | 0.37 | 0.36 | 0.33 | 0.31 | 0.28 | 0.25 | 0.20 | 0.04 | / |
| | 0.7 | 0.28 | 0.27 | 0.24 | 0.22 | 0.18 | 0.03 | / | / | / |
| | 0.8 | 0.19 | 0.17 | 0.14 | / | / | / | / | / | / |
| | 0.9 | 0.09 | 0.01 | / | / | / | / | / | / | / |
| 0.2 | 0.1 | 0.87 | 0.82 | 0.77 | 0.72 | 0.66 | 0.60 | 0.54 | 0.46 | 0.37 |
| | 0.2 | 0.79 | 0.75 | 0.70 | 0.65 | 0.60 | 0.55 | 0.49 | 0.43 | 0.34 |
| | 0.3 | 0.71 | 0.67 | 0.63 | 0.59 | 0.54 | 0.49 | 0.44 | 0.38 | 0.31 |
| | 0.4 | 0.62 | 0.59 | 0.55 | 0.51 | 0.47 | 0.43 | 0.39 | 0.34 | 0.27 |
| | 0.5 | 0.53 | 0.50 | 0.47 | 0.44 | 0.40 | 0.36 | 0.32 | 0.28 | 0.22 |
| | 0.6 | 0.43 | 0.41 | 0.38 | 0.35 | 0.32 | 0.28 | 0.23 | 0.05 | / |
| | 0.7 | 0.33 | 0.31 | 0.28 | 0.25 | 0.21 | 0.04 | / | / | / |
| | 0.8 | 0.22 | 0.20 | 0.17 | / | / | / | / | / | / |
| | 0.9 | 0.11 | 0.02 | / | / | / | / | / | / | / |
| 0.4 | 0.1 | 0.89 | 0.84 | 0.79 | 0.74 | 0.68 | 0.62 | 0.55 | 0.47 | 0.37 |
| | 0.2 | 0.83 | 0.78 | 0.73 | 0.68 | 0.63 | 0.57 | 0.51 | 0.44 | 0.35 |
| | 0.3 | 0.76 | 0.71 | 0.67 | 0.63 | 0.58 | 0.53 | 0.47 | 0.41 | 0.33 |
| | 0.4 | 0.68 | 0.64 | 0.60 | 0.56 | 0.52 | 0.47 | 0.42 | 0.37 | 0.30 |
| | 0.5 | 0.59 | 0.56 | 0.53 | 0.49 | 0.45 | 0.41 | 0.36 | 0.31 | 0.24 |
| | 0.6 | 0.50 | 0.47 | 0.44 | 0.41 | 0.37 | 0.33 | 0.27 | 0.07 | / |
| | 0.7 | 0.39 | 0.37 | 0.34 | 0.30 | 0.26 | 0.06 | / | / | / |
| | 0.8 | 0.28 | 0.25 | 0.21 | / | / | / | / | / | / |
| | 0.9 | 0.14 | 0.02 | / | / | / | / | / | / | / |
| 0.6 | 0.1 | 0.91 | 0.86 | 0.81 | 0.75 | 0.69 | 0.63 | 0.56 | 0.48 | 0.38 |
| | 0.2 | 0.86 | 0.82 | 0.77 | 0.71 | 0.66 | 0.60 | 0.53 | 0.46 | 0.36 |
| | 0.3 | 0.81 | 0.77 | 0.72 | 0.67 | 0.62 | 0.56 | 0.50 | 0.43 | 0.35 |
| | 0.4 | 0.75 | 0.71 | 0.66 | 0.62 | 0.57 | 0.52 | 0.47 | 0.40 | 0.32 |
| | 0.5 | 0.68 | 0.64 | 0.60 | 0.56 | 0.52 | 0.47 | 0.42 | 0.36 | 0.28 |
| | 0.6 | 0.59 | 0.56 | 0.52 | 0.48 | 0.44 | 0.39 | 0.33 | 0.10 | / |
| | 0.7 | 0.49 | 0.46 | 0.42 | 0.38 | 0.33 | 0.08 | / | / | / |
| | 0.8 | 0.36 | 0.33 | 0.28 | / | / | / | / | / | / |
| | 0.9 | 0.19 | 0.03 | / | / | / | / | / | / | / |
| 0.8 | 0.1 | 0.93 | 0.88 | 0.82 | 0.77 | 0.71 | 0.64 | 0.57 | 0.49 | 0.38 |
| | 0.2 | 0.90 | 0.85 | 0.80 | 0.75 | 0.69 | 0.63 | 0.56 | 0.48 | 0.38 |
| | 0.3 | 0.87 | 0.83 | 0.78 | 0.72 | 0.67 | 0.61 | 0.54 | 0.46 | 0.37 |
| | 0.4 | 0.84 | 0.79 | 0.74 | 0.69 | 0.64 | 0.58 | 0.52 | 0.44 | 0.35 |
| | 0.5 | 0.79 | 0.75 | 0.70 | 0.65 | 0.60 | 0.55 | 0.48 | 0.41 | 0.33 |
| | 0.6 | 0.73 | 0.69 | 0.64 | 0.60 | 0.55 | 0.49 | 0.42 | 0.16 | / |
| | 0.7 | 0.65 | 0.61 | 0.56 | 0.51 | 0.45 | 0.14 | / | / | / |
| | 0.8 | 0.52 | 0.48 | 0.42 | / | / | / | / | / | / |
| | 0.9 | 0.32 | 0.06 | / | / | / | / | / | / | / |

TABLE 3. INDICES OF RELATIVE PRODUCTIVITY ( IRP )

| $x_m^*/x_m'$ \ $\alpha$ (IRP, $\beta$) | | (cutting ratio; %) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 10 | 20 | 30 | 40 | 50 | 60 | 70 | 80 | 90 |
| 0.0 | 0.1 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.08 | 0.08 | 0.08 | 0.07 |
| | 0.2 | 0.16 | 0.16 | 0.16 | 0.16 | 0.16 | 0.15 | 0.15 | 0.14 | 0.12 |
| | 0.3 | 0.21 | 0.21 | 0.21 | 0.21 | 0.20 | 0.20 | 0.19 | 0.18 | 0.16 |
| | 0.4 | 0.24 | 0.24 | 0.24 | 0.24 | 0.23 | 0.23 | 0.22 | 0.21 | 0.19 |
| | 0.5 | 0.25 | 0.25 | 0.25 | 0.24 | 0.24 | 0.23 | 0.22 | 0.21 | 0.18 |
| | 0.6 | 0.24 | 0.24 | 0.24 | 0.23 | 0.22 | 0.21 | 0.19 | 0.04 | / |
| | 0.7 | 0.21 | 0.21 | 0.20 | 0.19 | 0.17 | 0.03 | / | / | / |
| | 0.8 | 0.16 | 0.15 | 0.13 | / | / | / | / | / | / |
| | 0.9 | 0.08 | 0.01 | / | / | / | / | / | / | / |
| 0.2 | 0.1 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.08 | 0.08 | 0.07 |
| | 0.2 | 0.17 | 0.17 | 0.17 | 0.16 | 0.16 | 0.16 | 0.15 | 0.14 | 0.12 |
| | 0.3 | 0.22 | 0.22 | 0.22 | 0.22 | 0.22 | 0.21 | 0.20 | 0.19 | 0.17 |
| | 0.4 | 0.26 | 0.26 | 0.26 | 0.26 | 0.25 | 0.25 | 0.24 | 0.22 | 0.20 |
| | 0.5 | 0.28 | 0.28 | 0.27 | 0.27 | 0.27 | 0.26 | 0.25 | 0.23 | 0.20 |
| | 0.6 | 0.27 | 0.27 | 0.27 | 0.26 | 0.25 | 0.24 | 0.22 | 0.05 | / |
| | 0.7 | 0.24 | 0.24 | 0.23 | 0.22 | 0.20 | 0.04 | / | / | / |
| | 0.8 | 0.19 | 0.18 | 0.16 | / | / | / | / | / | / |
| | 0.9 | 0.10 | 0.02 | / | / | / | / | / | / | / |
| 0.4 | 0.1 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.08 | 0.08 | 0.07 |
| | 0.2 | 0.17 | 0.17 | 0.17 | 0.17 | 0.17 | 0.16 | 0.16 | 0.15 | 0.13 |
| | 0.3 | 0.24 | 0.24 | 0.24 | 0.23 | 0.23 | 0.23 | 0.22 | 0.20 | 0.18 |
| | 0.4 | 0.29 | 0.28 | 0.28 | 0.28 | 0.28 | 0.27 | 0.26 | 0.24 | 0.22 |
| | 0.5 | 0.31 | 0.31 | 0.31 | 0.31 | 0.30 | 0.29 | 0.28 | 0.26 | 0.22 |
| | 0.6 | 0.32 | 0.31 | 0.31 | 0.30 | 0.30 | 0.28 | 0.25 | 0.07 | / |
| | 0.7 | 0.29 | 0.29 | 0.28 | 0.27 | 0.24 | 0.06 | / | / | / |
| | 0.8 | 0.23 | 0.22 | 0.20 | / | / | / | / | / | / |
| | 0.9 | 0.13 | 0.02 | / | / | / | / | / | / | / |
| 0.6 | 0.1 | 0.10 | 0.10 | 0.09 | 0.09 | 0.09 | 0.09 | 0.09 | 0.08 | 0.07 |
| | 0.2 | 0.18 | 0.18 | 0.18 | 0.18 | 0.18 | 0.17 | 0.16 | 0.15 | 0.13 |
| | 0.3 | 0.26 | 0.26 | 0.25 | 0.25 | 0.25 | 0.24 | 0.23 | 0.22 | 0.19 |
| | 0.4 | 0.32 | 0.31 | 0.31 | 0.31 | 0.31 | 0.30 | 0.29 | 0.27 | 0.23 |
| | 0.5 | 0.36 | 0.36 | 0.35 | 0.35 | 0.34 | 0.33 | 0.32 | 0.30 | 0.25 |
| | 0.6 | 0.37 | 0.37 | 0.37 | 0.36 | 0.35 | 0.34 | 0.31 | 0.10 | / |
| | 0.7 | 0.36 | 0.36 | 0.35 | 0.33 | 0.31 | 0.08 | / | / | / |
| | 0.8 | 0.30 | 0.29 | 0.27 | / | / | / | / | / | / |
| | 0.9 | 0.18 | 0.03 | / | / | / | / | / | / | / |
| 0.8 | 0.1 | 0.10 | 0.10 | 0.10 | 0.10 | 0.09 | 0.09 | 0.09 | 0.08 | 0.07 |
| | 0.2 | 0.19 | 0.19 | 0.19 | 0.19 | 0.18 | 0.18 | 0.17 | 0.16 | 0.14 |
| | 0.3 | 0.28 | 0.28 | 0.27 | 0.27 | 0.27 | 0.26 | 0.25 | 0.23 | 0.20 |
| | 0.4 | 0.35 | 0.35 | 0.35 | 0.35 | 0.34 | 0.33 | 0.32 | 0.30 | 0.26 |
| | 0.5 | 0.42 | 0.41 | 0.41 | 0.41 | 0.40 | 0.39 | 0.37 | 0.35 | 0.30 |
| | 0.6 | 0.46 | 0.46 | 0.46 | 0.45 | 0.44 | 0.42 | 0.39 | 0.16 | / |
| | 0.7 | 0.48 | 0.47 | 0.46 | 0.45 | 0.42 | 0.14 | / | / | / |
| | 0.8 | 0.44 | 0.43 | 0.40 | / | / | / | / | / | / |
| | 0.9 | 0.30 | 0.06 | / | / | / | / | / | / | / |

EXAMPLE 1

In a natural forest population of Picea asperata in Gansu province in China, we have obtained the following parameters of the growth curve:

$$U_c^* = 0.04 \ year^{-1} \ , \quad X_m^* = 400 \ M^3/ha \ , \quad X_m^*/X_m' = 0 \ .$$

If we would like to cut the forest at Xi=200 $M^3$/ha and set a cutting ratio as 40%, how many years do we have to wait for the forest to be maintained in a stable state and how much are the cutting intensity and the productivity?

From Table 1 we can find out the index of IRCP under $\alpha$=40%, $X_m^*/X_m'$=0, $\beta$=200/400 = 0.5:

$$IRCP = 1.02$$

The harvested cycle period = $1.02/U_c^*$ = 1.02/0.04 = 25.5 years; From Table 2 we can find out the index of IRCI under $\alpha$=40%, $X_m^*/X_m'$=0, $\beta$=0.5:

$$IRCI = 0.39$$

The cutting intensity = $0.39 \cdot U_c^*$ = 0.39 x 0.04 = 1.6%/years; From Table 3 we can find out the index of IRP under $\alpha$=40%, $X_m^*/X_m'$=0, $\beta$=0.5:

$$IRP = 0.24$$

The productivity = $0.24 \cdot U_c^* X_m^*$ = 0.24 x 0.04 x 400 = 3.8 $M^3$/ha·year.

EXAMPLE 2

In a natural forest population of Korean pine in Jilin province in China, we have obtained the following parameters of the growth curve:

$$U_c^* = 0.03 \ year^{-1} \ , \quad X_m^* = 400 \ M^3/ha \ , \quad X_m^*/X_m' = 0.8 \ .$$

If we would like to cut the forest in a cutting ratio of 20%, which stage is the best for the largest harvest (ie the productivity is the maximum) ? and in this cutting method, can you calculate the harvested cycle period, the cutting intensity and the productivity?

From Table 3 we find the best state is in $\beta$=0.7 where the index of IRP is equal to 0.47 (largest) when $X_m^*/X_m'$=0.8 and $\alpha$=20%

ie $$X_2 = \beta X_m^*/(1-0.5\alpha) = 0.7 \times 400/(1-0.5\times 0.2) = 311 \ M^3/ha \ ,$$

in which the productivity is the maximum.

The productivity = $0.47 \cdot U_c^* X_m^*$ = 0.47 x 0.03 x 400 = 5.6 $M^3$/ha;

From Table 1 we can find out the index of IRCP:

$$IRCP = 0.33$$

The harvested cycle period = 0.33/$U_c^*$ = 0.33/0.03 = 11 years;

From Table 2 we can find out the index of IRCI:

$$IRCI = 0.61$$

The cutting intensity = 0.61·$U_c^*$ = 0.61 × 0.03 = 1.8%/year.

(B) LIST OF SYMBOLS

| | |
|---|---|
| $t$ | time (year) |
| $t_1, t_2$ | times at point 1 and point 2 on the integral curve (year) |
| $\Delta t$ | harvested cycle period needed for a stable state; $\Delta t = t_2 - t_1$ |
| $Uc$ | growth velocity parameter ($year^{-1}$) |
| $Uc^*$ | increment velocity parameter in the natural condition ($year^{-1}$) $Uc^* = Uc - D$ |
| $Uc^{**}$ | increment velocity parameter in a managed condition ($year^{-1}$) $Uc^{**} = Uc^* - D^*$ |
| $X$ | population density ($M^3/ha$) |
| $X_1, X_2$ | population densities after cutting and before cutting ($M^3/ha$) |
| $\Delta X$ | cutting amount; $\Delta X = X_2 - X_1$ |
| $Xm$ | carrying capacity ($M^3/ha$) |
| $Xm^*$ | maximum population density in the natural condition ($M^3/ha$) $Xm^* = Xm(Uc - D)/(Uc - D \cdot Xm/Xm')$ |
| $Xm^{**}$ | population density with dynamic equilibrium in a managed forest $Xm^{**} = Xm^*(Uc^* - D^*)/(Uc^* - D^* Xm^*/Xm')$ |
| $Xm'$ | a parameter concerning the efficiency of nutrient utilization by an organism ($M^3/ha$) |
| $Xi$ | the population density at the middle point between $X_1$ and $X_2$ |
| $D$ | death velocity parameter ($year^{-1}$) |
| $D^*$ | cutting intensity allowed by a sustained management (%/year) |
| $D^*_{0.5}$ | value of $D^*$ at $0.5Xm^*$ |
| $\lim_{\Delta t \to 0} D^*$ | value of $D^*$ at continuous selective cutting |
| $\alpha$ | cutting ratio (%) |
| $\beta$ | relative cutting position $\beta = Xi/Xm^*$ |
| $\beta_m$ | value of $\beta$ at the inflexion point |
| IRCP | index of relative cycle period; $IRCP = \Delta t \cdot Uc^*$ |
| IRCI | index of relative cutting intensity; $IRCI = D^*/Uc^*$ |
| IRP | index of relative productivity; $IRP = \text{productivity}/Uc^* Xm^*$ |

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